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Past and Projected Future Changes in Species Distributions as a Consequence of Climate Change

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Past and Projected Future Changes in Species Distributions as a Consequence of Climate Change

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Past and Projected Future Changes in Species Distributions as a Consequence of Climate Change

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Recent climate change has already caused range shifts for many species, and future changes in the climate will likely lead to additional large-scale changes in species assemblages and richness. Most research into the effects of past climate change on species distributions has not accounted for the possibility of additional drivers opposing or working in tandem with climate. Failure to identify additional drivers may lead to inaccurate estimates of the contribution of climate change. Similarly, models used to build future projections of species' distributions do not incorporate uncertainty into the estimates, which is inherently generated by several user defined parameters during the model building process. Using both field and modeling approaches, I quantified multiple drivers of past range changes in a community of Plethodontidae salamanders in the southern Appalachian Mountains and created future projections, which incorporated estimates of uncertainty, for the salamanders and several species endemic to the southwestern United States. Results from the field component demonstrated that salamanders expanded their elevational ranges due to two independent drivers: forest maturation and a slight cooling trend in the region. The modeling approach suggested that the majority of suitable climate space for salamander species in the southern Appalachian Mountains and several endemic species in the southwestern United States

may decrease by mid-century. Further, the results indicate that four model parameters contributed most of the uncertainty to future projections.

Table of Contents

Chapter 1: Introduction & Summary 1

Chapter 2: Recent elevational range expansions in plethodontid salamanders in the southern Appalachian Mountains 4

Abstract 4

Introduction 5

Methods 7

Historical data 7

Fieldwork 7

Identification in Nantahala Mountains 9

Data used in analyses 9

Data analysis 11

Results 13

Elevational range changes 13

Regression models 13

Discussion 14

Expansions with forest maturation and climate cooling 14

Complex responses for foothill species 16

Sampling effort and assumptions 17

Conclusions 18

Tables & Figures 20

Chapter 3: Sources of Uncertainty in Biodiversity Projections under a Rapidly Changing Climate 28

Abstract 28

Introduction 29

Methods 31

Species data 31

Statistical modeling methods 32

Environmental data 32

Current 32
Future 33
Spatial modeling regions....34
Pseudo-absence and training replicates 35
Data analysis 35
Results....37
Current and future projections 37
Evaluation metrics 38
Discussion 38
Tables & Figures....42
Chapter 4: Shifting biodiversity hotspots in the southwestern United States due to projected climate change....49
Abstract....49
Introduction....49
Methods....51
Species data....51
Current climate data....52
Future climate data....53
Spatial modeling region 54
Species distribution modeling method....54
Training and pseudo-absence replicates 55
ANOVA 55
Analysis for all 164 species 56
Results....58
ANOVA 58
AUC statistics 58
'Realized' geographical extent 59
'Potential' geographic extent 60
Discussion 60
Tables & Figures....64

Appendix.....71

References.....98

Vita……...108

Chapter 1: Introduction & Summary

The driving motivation of this dissertation is to understand the role of recent climate change in affecting the distributions of species, as well as develop modeling techniques to more accurately predict future changes in distribution. Recent climate change has already caused range shifts for many species (Parmesan & Yohe, 2003; Root et al., 2003; Parmesan, 2006), and future changes in the climate will likely lead to additional large-scale changes in species assemblages and richness (Warren et al., 2013). Thus, several research efforts have been undertaken to better understand the role of climate in recent changes in species' distributions (Parmesan & Yohe, 2003; Root et al., 2003; Parmesan, 2006) and how future changes in climate could further impact species (Bakkenes et al., 2002; Erasmus et al., 2002; Peterson et al., 2002; Thuiller et al., 2005b; Araujo et al., 2006).

While many studies provide compelling evidence for changes in climate being an important driver in species' distributional changes (Parmesan & Yohe, 2003; Root et al., 2003; Parmesan, 2006), most rarely consider multiple drivers. A single factor approach has the potential to incorrectly estimate the role of climate in distributional changes (Parmesan et al., 2011), which can ultimately lead to poor estimates of species' sensitivity to climate and projections. In addition to failing to account for multiple drivers, most future projections created with species distribution models fail to explore model uncertainty due to multiple user defined parameters and settings. A few studies have explored and quantified the uncertainty generated by a one or two model settings (Araujo & Guisan, 2006; Barry & Elith, 2006; Elith et al., 2006; Guisan et al., 2006b;

Heikkinen et al., 2006; Dormann et al., 2008; Graham et al., 2008); however few studies, to the author's knowledge, have considered several factors at the same time.

In this dissertation, I approached the study of climate change effects on species distributions by first conducting a field study to quantify the role of past change and additional drivers on range changes in several species of Plethodontidae salamanders. Then I used species distribution models, which incorporate several sources of uncertainty, to estimate the future distributions of salamanders in the southern Appalachian Mountains and 164 endemic species in the southwestern United States. By taking this multifaceted approach, I was able to (1) more accurately determine the role of climate in recent changes in distribution and (2) provide more accurate projections of future change.

In Chapter 2, I conducted a field study in the southern Appalachian Mountains to assess the impacts of past climate and forest stand change to a community of Plethodontidae salamanders living from 518 to 2036 m elevation. My study quantified elevational range changes, using data collected in the 1940s by Nelson Hairston, and used correlational analyses to examine which factors were significant drivers. By quantifying the past impacts of climate change, better future projections for salamanders can be made. Additionally, the results indicated that by carefully managing forests, the impacts from future climate change can potentially be reduced.

For Chapter 3, I used species distribution models to project the distributions of sixteen species of Plethodontidae salamanders endemic to the southern Appalachian Mountains. These projections incorporated and quantified several sources of uncertainty to determine which were the most important. Overall, the study provided future projections for the several species of salamanders, and also indicated which sources of uncertainty should be incorporated into most species modeling efforts.

Finally in Chapter 4, I applied the findings from the previous modeling study in Chapter 3 to create a suite of future projections for 164 species endemic to a five state region in the southwestern United States. Overall, this allowed me to provide low and high estimates of expected change for these species, including the identification of regions of high species richness today and into the future, as well as estimates of range change and turnover. This study further demonstrated that species distribution modeling efforts for climate change should incorporate multiple sources of uncertainty into projections.

Chapter 2: Recent elevational range expansions in plethodontid salamanders in the southern Appalachian Mountains[1]

ABSTRACT

Approximately 32.5% of all amphibian species are globally threatened, and amphibian extinctions have been recorded worldwide. Individual studies rarely give full consideration to multiple potential drivers of observed biological change, instead tending to attribute changes to a single driver. Here, I tested for impacts of land use and climate change on range changes in a community of plethodontid salamanders living from 518 to 2036 m elevation in a global hotspot for amphibian diversity in the southern Appalachian Mountains. I resurveyed 18 elevational transects that had originally been surveyed by Nelson Hairston in 1940, 1947, and 1949. I recorded range changes for nine species that Hairston studied and determined the extent to which the recorded expansions or contractions could be attributed to changes in forest stand, climate, and competition, singly or in combination. 'Montane' species, which occur only on mountaintops, had expanded their lower elevational limits downwards. 'Foothill' species, which occur at lower elevations than montane species, had expanded their upper elevational limits upwards. For montane species these downward expansions appear to be the result of two processes: local cooling of the climate and maturation of forests after the cessation of large-scale logging operations c. 80 years ago. In contrast, changes in upper elevational range limits of foothill species are probably the result of a suite of complex and interacting drivers, including, but not limited to, maturation of forests, changes in climate, and interactions with other species.

[1] Moskwik M (2014) Recent elevational range expansions in plethodontid salamanders (Amphibia: Plethodontidae) in the southern Appalachian Mountains. *Journal of Biogeography*, **41**, 1957-1966.

INTRODUCTION

Amphibian population extinctions have been recorded worldwide and 32.5% of all amphibian species are globally threatened (Stuart et al., 2004). These declines have been attributed to a variety of anthropogenic factors including habitat destruction, over-exploitation, chemical contaminants, disease, UV-B radiation, introduced species, and climate change (Collins & Storfer, 2003). While many studies provide compelling evidence for a particular factor being the driver of changes, most studies rarely consider multiple potential drivers.

The southern Appalachian Mountains are an ideal region in which to study multiple threats on amphibians because there has been a spatially varied history of forest disturbances and climate change. Additionally, this region has a high diversity of plethodontid salamanders, with many endemic species (Petranka, 1998). A few recent studies have documented declines in population abundances, but were unable to (Caruso & Lips, 2013) or did not attempt to provide a particular factor causing the changes (Highton, 2005). Declines could have negative impacts on stream communities in the region because plethodontid salamanders are important predators, playing key roles in the cycling of nutrients (Davic & Welsh, 2004; Walton & Steckler, 2005; Walton et al., 2006).

There have been several anthropogenic disturbances to the southern Appalachian forests during the late 19th and the 20th centuries. Specifically, these forests were clearcut extensively from the late 1800s until the 1920s (Williams, 1989; Yarnell, 1998). Then, from the late 19th century until about 1930, high-intensity, stand-replacing fires were common owing to slash logging practices (Brose et al., 2001). A third major disturbance to these forests occurred in the late 1920s and 1930s when *Cryphonectria parasitica* (chestnut blight) eliminated *Castanea dentata* (American chestnut; Elliot &

Swank, 2008). Today, following the cessation of extensive logging operations, the suppression of fire, and the replacement of *Castanea dentata* by other woody species, new forest communities have grown up and matured in this region. However, some changes continue to occur: coniferous *Abies fraseri* (Fraser fir) and *Tsuga canadensis* (Canadian hemlock) forests have recently declined as a result of infestations by introduced *Adelges piceae* (balsam woolly adelgid) and *Adelges tsugae* (hemlock woolly adelgid), respectively.

Salamanders are sensitive to changes in forest structure. Specifically, lower plethodontid species richness and abundance have been documented in recently logged versus mature forests (Petranka et al., 1993, 1994; Ash, 1997; Herbeck & Larsen, 1999; Grialou et al., 2000; Ashton et al., 2006). Loss of forest canopy decreases leaf litter dry mass and depth (Ash, 1995) and the moisture contents of both soil (Petranka et al., 1994; Ash, 1997; Herbeck & Larsen, 1999) and leaf litter (Buckner & Shure, 1985; Ash, 1995), while at the same time increasing soil temperature (Petranka et al., 1994; Ash, 1997; Herbeck & Larsen, 1999). All of these changes represent deterioration of habitat quality for salamanders (Petranka et al., 1994; Ash, 1995).

In addition to changes in forest age and composition, the region recorded a slight decrease in the average annual temperature during the 20th century (IPCC, 2001; Rogers, 2012). Many plethodontid salamanders are known to be sensitive to climate, and high species richness is positively linked to cool, moist climates (Marshall & Camp, 2006; Kozak & Wiens, 2010). Additionally, physiological experiments with montane plethodontids have demonstrated that low-elevation populations are living near their upper thermal tolerance limits (Bernardo & Spotila, 2006; Bernardo et al., 2007).

Any contribution to documenting changes in amphibian distribution and abundance requires a historical dataset as a baseline. I followed a baseline set by

Hairston (1949, 1951), who surveyed plethodontid salamanders across 19 elevational transects in the southern Appalachian Mountains of North Carolina, South Carolina and Tennessee in 1940, 1947, and 1949. I resurveyed 18 of these transects and recorded range changes for nine species (formerly five species) that Hairston studied. I used multiple regression models to examine the relationship between observed elevational range expansions or contractions of plethodontid salamanders in the southern Appalachian Mountains and changes in forest stand and climate since Hairston's surveys.

METHODS

Historical data

In the summers of 1940 and 1947 Hairston (1949) surveyed six elevational transects in the Black Mountains of North Carolina to examine the elevational limits of several Plethodontidae species. Specifically, in 1940 he surveyed Transects 2, 4, and 5 and in 1947 Transects 1, 3 (Figure 2.1), and Cane River. Then in the summer of 1949 Hairston (1951) established and surveyed an additional 13 elevational transects in the Balsam, Nantahala, and Great Smoky Mountains and Jocassee Gorges (Figure 2.1). Since Hairston's work, *Plethodon jordani* and *Plethodon glutinosus* have each been separated into a complex of species (Highton, 1983; Highton et al., 1989; Highton & Peabody, 2000; Table 2.1).

Fieldwork

For this study, I concentrated on the terrestrial *Plethodon* species examined by Hairston: *Plethodon jordani*, *Plethodon metcalfi*, *Plethodon montanus*, *Plethodon shermani*, *Plethodon teyahalee*, *Plethodon cylindraceus*, and *Plethodon yonahlossee* (Amphibia: Plethodontidae). I also regularly encountered *Desmognathus carolinensis* and *Desmognathus organi* in the Black Mountains and recorded their presence on

transects and plots, allowing me to estimate their elevational range limits. I classified the *P. jordani* complex and *D. organi* as 'montane' species because they occur at the highest elevation on transects, and the *P. glutinosus* complex and *P. yonahlossee* as 'foothill' species because their upper elevational limits do not reach the highest elevation on transects.

Based on details in published manuscripts (Hairston, 1949, 1951), I was able to resurvey 18 of the Hairston transects (Figure 2.1; for specific location details see Table A.1). I was unable to resurvey the Cane River Transect (Hairston 1949, 1951) because of private property restrictions and the lower half of Transect 18 owing to the creation of Lake Jocassee in 1973. Additionally, small sections of Transects 15 and 17 were not surveyed because of private property restrictions. These unsurveyed sections did not impact the delineation of elevational range limits for the *P. jordani* and *P. glutinosus* complexes because both were recorded beyond the boundaries of all private property.

During June and July 2011 these 18 transects were walked once by two to four people during daylight hours. Natural cover objects were continuously lifted along transects to check for the presence of salamanders. When a salamander was found, it was identified to species and its location recorded on a Garmin 60CSX GPS (Garmin International Inc., Olathe, KS, USA). After preliminary range boundaries were identified for each species (i.e., the highest and lowest elevation recorded for each species), 30 m × 40 m plots were placed at those range boundaries. To confirm range boundaries, plots were also placed 30 m higher in elevation for upper elevational limits and 30 m lower in elevation for lower elevational limits. However, no plots were placed beyond the maximum or minimum elevations of Hairston's transects. Additionally, if range contractions were recorded, then additional plots were placed at 90-m elevation intervals within the area of contraction to provide additional confirmation of absence. On each

plot all natural cover objects (e.g. logs, bark, decaying wood), excluding leaf litter, were checked by two to four people for salamanders.

Identification in Nantahala Mountains

Plethodon shermani and *P. teyahalee* hybridize where their distributions overlap in the Nantahala Mountains (Highton & Peabody, 2000). Hairston (1951) suggested that a hybrid zone was present, but categorized all individual salamanders he encountered as either *P. jordani* (currently *P. shermani*) or *P. glutinosus* (currently *P. teyahalee*). I implemented the scoring system he developed later to help categorize hybrid salamanders (Hairston et al., 1992). Individuals were given a zero to three score for the amount of red on the legs and a zero to three score for white spotting on the body. Scores for both attributes were used to assign individuals to species (Table A.2). Upper elevational limits for *P. teyahalee* were delineated based on salamanders scoring at most one for red on the legs and at least two for white spotting on the body. These individuals had small red spots on the hind legs, extensive white spotting on the sides of the body, and black bodies. In contrast, salamanders with at least two for red on the legs and at most two for white spots were used to delineate the lower elevational limits for *P. shermani*. These individuals had large patches of red on both legs, small, frosty blotches on the sides, and grey bodies.

Data used in analyses

One of Hairston's objectives was to accurately determine the elevational range limits of species (i.e., last recorded individual of each species), thus he did not quantify the abundance of species or provide detailed notes about sampling effort. Therefore, to ascertain elevational range changes for species, I compared the recorded elevational range limits in 2011 to those recorded by Hairston (1949, 1951) in the 1940s. For all

statistical analyses, elevational range changes were examined for the lower elevational limits of montane species and the upper elevational limits of foothill species.

For the *P. jordani* complex, elevational range limit data from four transects were not included in the statistical analyses, yielding a sample size of 14 (Table 2.2). Hairston (1951) and I both recorded the *P. jordani* complex at the bottom of Transects 16 and 17. Its continued presence at the lowest elevation on these transects in 2011 demonstrates that the species complex has not disappeared; however, these locations may not be the true elevational limits (i.e., elevational range changes could have occurred at lower elevations). Therefore, the data for the *P. jordani* complex on these transects were excluded from the statistical analyses. I was also unable find the lower elevational limits of the *P. jordani* complex on Transect 18 owing to the creation of Lake Jocassee. Finally, Hairston (1951) did not provide the lower elevational limit of the *P. jordani* complex on Transect 4, so the 2011 data from this transect were not included in the statistical analyses.

For the *P. glutinosus* complex, elevational range limit data from two transects were not used in the analyses, yielding a sample size of 16 (Table 2.2). Hairston (1951) and I recorded the *P. glutinosus* complex at the highest elevation on Transect 18. This demonstrates that the species complex has not disappeared on this transect; however, the upper elevational range limit of this species complex could have changed at higher elevations. Thus, data for the *P. glutinosus* complex on Transect 18 were excluded from the analyses. Data from Transect 4 for the *P. glutinosus* complex were also excluded because no upper elevational limit was provided by Hairston (1951). For *P. yonahlossee*, *D. organi* and *D. carolinensis*, I followed Hairston (1949) and pooled their elevational range limit data for Transects 2 and 4, reducing the sample size for each species from five to four (Table 2.2).

Data analysis

The elevations of individual salamanders and plot centres were obtained in ArcGIS 10.0 (ESRI, Redlands, CA, USA) by overlaying coordinates on a 1/9 arc-second digital elevation model (DEM) for North Carolina and 1/3 arc-second DEM for Tennessee, available from United States Geological Survey, Earth Resources Observation and Science (EROS) Center, Sioux Falls, SD, USA. I conducted statistical analyses using R 2.15.1 (R Core Team, 2012). To determine whether the lower elevational limits of montane species significantly changed between the 2011 resurvey and Hairston's surveys (Hairston, 1949, 1951), I pooled the data from the *P. jordani* complex (n = 14) and *D. organi* (n = 4) to yield a sample size of 18 and conducted a paired t-test. Similarly, I used a paired t-test for the upper elevational limits of foothill species, pooling the data of the *P. glutinosus* complex (n = 16) and *P. yonahlosee* (n = 4) to yield a sample size of 20. In case transect location was a confounding factor, I also conducted a repeated measures analysis of variance (ANOVA), with transect as the within group factor, for both montane and foothill species separately.

To quantify the changes in climate since Hairston's surveys, average annual maximum and minimum temperature and annual precipitation grids, at a resolution of 4 km × 4 km, were downloaded from the PRISM Climate Group (http://www.prism.oregonstate.edu/) for the 10 years prior to each survey date (i.e., 1930–1939, 1937–1946, 1939–1948, and 2001–2010). Temperature and precipitation grids were averaged for the 10-year period. Ten-year averages were used to remove the effects of any extreme or unusual years. Finally, the maximum and minimum temperature and precipitation grids corresponding to the time of Hairston's surveys were subtracted from their respective 2001–2010 grids to obtain trends for transects (Table 2.3). Temperature and precipitation trends for individual species were obtained by

averaging values from grid cells where elevational range changes occurred on each transect, not over the entire transect because in many cases different sections showed different trends (e.g. high elevations warmed, whereas low elevations cooled).

I obtained forest stand age data from the United States Forest Service office in Asheville, NC, USA, for transects in the Black, Balsam and Nantahala Mountains, except for Transect 1 in the Black Mountains. Using these data in ArcGIS 10.0, I recorded the forest stand age for the lower elevational limits of montane species and the upper elevational limits of foothill species during Hairston's surveys. I took the natural logarithm of forest stand age. Owing to the lack of stand age data for the Great Smoky Mountains and Transect 1, sample sizes were reduced to 12 for montane species and 14 for foothill species.

The 2011 elevational range limit for every species on each transect (i.e., lower elevational limits for montane and upper elevational limits for foothill species) was subtracted from its 1940, 1947 or 1949 elevational range limit, yielding elevational range change. These values were pooled for montane and foothill species separately. Then I conducted multiple regressions for both montane ($n = 12$) and foothill ($n = 14$) species separately to examine the relationship between the elevational range changes and the trends in minimum and maximum temperature and precipitation and the forest stand age during the Hairston surveys (1949, 1951). I also pooled the data from montane ($n = 12$) and foothill ($n = 14$) species to yield a sample size of 26 and conducted multiple regression using the same set of predictors. For all regression models, forward stepwise selection and Akaike's information criterion (AIC) were used for variable inclusion and final model selection.

RESULTS

Elevational range changes

Approximately 408.3 person hours, 132 plots, and 1750 salamanders were logged and recorded during the 2011 resurvey effort (Table 2.4; for individual plot data see Table A.3). A paired *t*-test ($P = 0.004$) and a repeated measures ANOVA ($P = 0.004$) indicated foothill species significantly expanded their upper elevational limits by an average of 143 ± 44 m (Figure 2.2a). Hairston's surveys recorded the *P. glutinosus* complex and *D. carolinensis* in the Black Mountains at the lowest elevation on transects. The 2011 resurvey also found both species at the lowest elevation on most transects, thus no overall contractions occurred (Figure 2.2b). Additionally, the lower elevational limits of *P. yonahlossee* changed little (Figure 2.2b).

The lower elevational limits for montane species significantly expanded downwards by an average of 215 ± 68 m, as indicated by a paired *t*-test ($P = 0.006$) and a repeated measures ANOVA ($P = 0.014$; Figure 2.2b). Additionally, the *P. jordani* complex, *D. organi* and *D. carolinensis* in the Black Mountains were recorded at the top of most transects in Hairston's surveys and in the 2011 resurvey; therefore, most upper elevational limits showed no contractions for these species (Figure 2.2a).

Regression models

When multiple regressions models were done separately for montane and foothill species, no significant models were found (i.e., all had P-values greater than 0.05). However, three significant models were found when the data from montane and foothill species were pooled. The 'best' model with the lowest AIC included forest stand age (slope = −145.5, P = 0.009) and average annual minimum temperature (slope = −146.9, P = 0.006) as significant predictors for range expansions (i.e., downward expansions for

montane species and upward expansions of foothill species; Table 2.5). A negative relationship with forest stand age indicates that elevational range expansions were greater in those forests that were young during Hairston's surveys. Additionally, a decrease in the average annual minimum temperature was associated with expansions downwards in montane species and upwards in foothill species. The two additional models which reached significance had higher AIC values. One included only forest stand age (slope = −128.9, P = 0.039; Figure 2.3a) and the other only average annual minimum temperature (slope = −132.3, P = 0.023; Figure 2.3b) as significant predictors.

DISCUSSION

Overall, this study shows that montane species significantly expanded downwards in elevation and foothill species significantly expanded upwards in elevation since the 1940s. These range expansions are largely consistent with local changes in forest structure as well as with changes in local temperature.

Expansions with forest maturation and climate cooling

One potential driver of the recorded expansions is the maturation of forests since Hairston's surveys in the 1940s. Specifically, during Hairston's surveys the forests were recovering from being heavily logged (Williams, 1989; Yarnell, 1998), suffering high-intensity fires (Brose et al., 2001), and die-off of *Castanea dentata* caused by an outbreak of *Cryphonectria parasitica* (Elliot & Swank, 2008).

During his fieldwork, Hairston (1951) even noted that some parts of transects were devoid of salamanders as a result of deforestation from either logging operations or fire. Additional anecdotal support for this hypothesis is provided by this study's finding of a relatively small downward expansion of the montane *P. jordani* in the Great Smoky Mountains, where little logging or fire occurred on transects (National Park Service,

2007), compared with my finding of large downward expansions of montane species at other sites that were heavily logged in the early 20th century.

Several studies have already documented reductions or complete losses of populations of several species of salamanders in the southern Appalachians as a result of disturbance, such as logging operations (Petranka et al., 1993, 1994; Ash, 1997; Herbeck & Larsen, 1999; Grialou et al., 2000; Ashton et al., 2006). Salamander declines and extirpations have been attributed to the loss of canopy and leaf litter (Ash, 1995), which lead to higher temperatures (Petranka et al., 1994; Ash, 1997; Herbeck & Larsen, 1999), greater temperature variability (Chen et al., 1993; Brooks & Kyker-Snowman, 2008), and lower moisture (Buckner & Shure, 1985; Petranka et al., 1994; Ash, 1997; Herbeck & Larsen, 1999) at ground level where forest plethodontids are active. However, this study suggests that losses of salamander populations may be greater at or near elevational range limits after heavy forest disturbance.

A second driver of the observed expansions is likely to be the documented slight cooling trend in the region (IPCC, 2001; Rogers, 2012). This regional cooling trend has been attributed to changes in ocean circulation patterns, cloud cover and soil moisture (Rogers 2012), but could have also been enhanced locally by forest regrowth and maturation. In this study, decreases in average annual minimum temperature were associated with downward elevational range expansions for montane species. A downward expansion of montane species in a cooling climate is supported by physiological studies (Bernardo & Spotila, 2006; Bernardo et al., 2007), which have demonstrated that several species of montane salamanders are sensitive to temperature.

This interpretation is also supported by the observed upward contraction of the montane *P. shermani* in the Nantahala Mountains in concert with a large increase in the average annual minimum temperature. Walls (2009) also attributed a similar contraction

of *P. shermani* at Coweeta Hydrologic Lab in the Nantahala Mountains with an increase in the average annual temperature.

To the author's knowledge, this study is the first to have recorded downward elevational range expansions of montane amphibian species in a regionally cooling climate. In contrast, previous studies have attributed either elevational range contractions (Raxworthy et al., 2008; Walls, 2009) or population declines (Whitfield et al., 2007; McMenamin *et al.*, 2008) to climate warming.

Complex responses for foothill species

Conversely, it is surprising to see upward range expansions in foothill species associated with a decrease in average minimum temperatures, as one would expect upward expansions to be associated with climate warming. Without setting up long-term experimental studies, I cannot provide an analytical explanation for this result. However, previous studies have suggested that interactions with montane species, which I was unable to account for in this study, may be an important factor in determining the upper elevational range limits of foothill species (Hairston, 1980; Hairston et al., 1992; Gifford & Kozak, 2011).

Several studies have shown that members of the *P. jordani* complex compete and, in one region, hybridize with members of the *P. glutinosus* complex. For example, in the Balsam Mountains an experimental study demonstrated that removing montane *P. metcalfi* from field plots resulted in a significant increase in the overall abundance of foothill species *P. teyahalee* (Hairston, 1980). Perhaps the clearest indication of competition being an important driver in the upper elevational range limits of *P. teyahalee* is in the Great Smoky Mountains. Both experimental field (Hairston, 1980) and modelling (Gifford & Kozak, 2011) studies have shown that montane *P. jordani* is a

superior competitor that excludes *P. teyahalee* from its habitats. Given this direct evidence for competition between these two species in this region, it is likely that the downward expansion of *P. jordani* directly drove the downward contraction of *P. teyahalee* by competitive exclusion. Further, hybridization in the Nantahala Mountains between *P. teyahalee* and montane *P. shermani* (Highton & Peabody, 2000) is an important factor in determining the upper elevational limits of pure *P. teyahalee* (Hairston et al., 1992). Thus, for foothill species upper elevational range limits could be the result of a suite of complex, interacting factors, including, but not limited to forest structure, climate, and interactions with other species.

Sampling effort and assumptions

An important assumption underlying interpretation of these results is that the 2011 resurvey and Hairston's surveys were similar in effort, allowing for direct comparison of the datasets. Hairston (1951) stated that as he walked transects, he checked frequently for salamanders at intervals no greater than 30.5 m. In addition, he spent extra time and effort near the elevational limits of species, notably spending 10 days on one transect to determine the elevational limits of two species. Other than this brief notation, he did not quantify his effort on transects. The 2011 effort attempted to duplicate Hairston's effort by continuously sampling the transects and establishing plots at species elevational range boundaries and at 30 m above for foothill and 30 m below for montane species. On many transects additional plots were sampled above or below the 30 m plot to confirm the elevational limits.

There is always a possibility that an observed range contraction could represent a detection error; however, the two small elevational range contractions used in the statistical analyses are supported by previous studies and thus are not likely to be a design

artefact. The downward contractions of foothill *P. teyahalee* in the Great Smoky Mountains are consistent with a previous study recording declines in this species (Caruso & Lips, 2013), and Hairston et al. (1992) recorded a similar upward range contraction of montane *P. shermani* at Coweeta Hydrological Laboratory in the Nantahala Mountains. Additionally, both contractions are associated with expansions in 'competitor' species (i.e., *P. teyahalee* in the Nantahala and montane *P. jordani* in the Great Smoky Mountains).

The very small changes recorded for the lower elevational range limits of *P. glutinosus* are probably the result of detection errors (i.e., false absences) on some transects by Hairston in the Balsam Mountains and the 2011 resurvey in the Black, Great Smoky, and Nantahala Mountains because this species complex is known to extend well below the lowest elevation of the Hairston transects. However, this does not affect any of my conclusions, as these data were not used in the statistical analyses (this study only examined changes in the upper elevational limits of the *P. glutinosus* complex).

Conclusions

In summary, almost all range limits showed expansions (i.e., lower elevational limits for montane and upper elevational limits for foothill species). Past forest disturbances, such as large-scale logging and fire, appear to have been detrimental to most salamanders at their elevational range limits, probably causing range contractions of many species by the time of Hairston's surveys in the 1940s. In the current study, montane species had generally expanded their lower elevational ranges in forests that were recovering from disturbance, and showed smaller range expansions, associated with regional cooling trends, in forests that had been mature at the time of Hairston's surveys. In contrast, documented changes in the upper elevational range limits of foothill species

are probably the result of a suite of complex and interacting drivers including competition from montane species that expanded downwards, as well as forest maturation and changes in climate (warming or cooling depending on location) that I was unable to assess quantitatively within the limits of this study.

This study demonstrates that montane species are sensitive to changes in both forest structure and climate. Therefore, carefully directed forest management could be an important addition to the growing suite of proactive measures that have been suggested for conservation efforts to help preserve plethodontid salamanders in the face of projected climate warming in the southern Appalachian Mountains during the 21st century (Milanovich et al., 2010).

TABLES & FIGURES

	Mountain range			
Category	Black	Balsam	Great Smoky	Nantahala
Montane	*Plethodon montanus** *Desmognathus organi*	*Plethodon metcalfi**	*Plethodon jordani**	*Plethodon shermani**
Foothill	*Plethodon yonahlosee*			
	Plethodon cylindraceus^{+}	*Plethodon teyahalee*$^{+}$	*Plethodon teyahalee*$^{+}$	*Plethodon teyahalee*$^{+}$

Table 2.1 The geographical distributions listed by mountain range for plethodontid salamander species examined in the southern Appalachians in this study. All montane species except *Desmognathus organi* are members of the *Plethodon jordani* complex (indicated with a *). All foothill species except *P. yonahlossee* are members of the *P. glutinosus* complex (indicated with a +). Jocassee Gorges is not included in the table; however, *P. metcalfi* and *P. teyahalee* occur there. *Desmognathus carolinensis* occurs over all elevations in the Black Mountains.

Taxon	Data used in statistical analyses	Elevations sampled (m)
P. jordani complex	Transects 1–3, 5–15	518–2036
D. organi	Transects 1–5	610–2036
P. glutinosus complex	Transects 1–3, 5–17	518–2036
P. yonahlossee	Transects 1–5	610–2036
D. carolinensis	Transects 1–5	610–2036

Table 2.2 For each species or complex of plethodontid salamanders surveyed in the southern Appalachian Mountains, the specific transects where elevational range data were used for statistical analyses are provided. For the *Plethodon jordani* complex and *Desmognathus organi* the lower elevational limits were used, whereas for the *P. glutinosus* complex, and *P. yonahlossee* the upper elevational limits were used. Additionally, the lower and upper elevational bounds across all listed transects are provided for each species or complex.

Mountain range	Trends from Hairston surveys to 2011 resurvey: Maximum temperature (°C)	Minimum temperature (°C)	Precipitation (mm)	Forest age during Hairston surveys (years)
Black	−1.3 ± 0.5	−0.7 ± 0.3	49 ± 16	57.6 ± 11.0
Balsam	0.3 ± 0.2	0.4 ± 0.4	−206 ± 62	35.8 ± 5.1
Great Smoky	−2.2 ± 0.4	−0.2 ± 0.1	60 ± 36	NA
Nantahala	−0.6 ± 0.3	1.2 ± 0.3	−86 ± 40	18.0 ± 3.7

Table 2.3 Average annual maximum and minimum temperature and precipitation trends averaged for all transects in each mountain range in the southern Appalachians (n = 5 for Black, n = 5 for Balsam, n = 4 for Great Smoky, and n = 3 Nantahala). Trends are the differences between the 10 years previous to Hairston's surveys in 1940, 1947, and 1949 and the 2011 resurvey. Additionally, the forest stand age (± one standard error) during Hairston's surveys (1949, 1951) are averaged for all transects in each mountain range. See Methods for specific calculations. NA in the table indicates data that were not available.

Mountain Range	Transect	Elevation (m)	*P. jordani* complex	*D. organi*	*P. glutinosus* complex	*P. yonahlosee*	Transect length (km)	Person hours	Number of plots
Black	1	732–1945	148	22	85	33	10.8	38	13
	2	914–2036	132	23	15	4	8.9	37.9	11
	3	823–1884	81	57	26	13	4.7	32.2	13
	4	610–1250	11	0	14	5	4.5	16.6	5
	5	823–1524	57	36	14	8	4.8	28.1	11
Balsam	6	945–1554	80		12		4.1	19.1	6
	7	945–1859	75		11		6.3	23.6	7
	8	945–1737	50		8		8.8	16	4
	16	1036–1692	62		8		5.4	13.5	4
	17	716–1615	104		26		16.2	25.5	5
Great Smoky	9	988–1341	113		12		0.8	13	5
	10	988–1158	33		5		2.1	12.5	4
	11	899–1295	14		7		1.9	10	4
	12	518–1554	73		7		9.3	28.4	10
Nantahala	13	701–1250	33		16		5.8	25.5	9
	14	648–1219	102		22		3.7	28.7	11
	15	689–1250	48		20		40.4	33.3	8
Jocassee Gorges	18	351–671	4		4		3.5	6.5	2

Table 2.4 The sampling effort and numbers of plethodontid salamanders encountered in surveys in the southern Appalachians is listed by mountain range and transect. Transect numbers follow Hairston (1951), except Transect 4, which is Sugar Cove. Specifically, for each transect the elevational range sampled and the number of salamanders of the *Plethodon jordani* and *P. glutinosus* complexes, *Desmognathus organi*, and *P. yonahlossee* are given. Additionally, the length, number of person hours, and plots are also provided. Small sections of Transects 15 and 17 were not walked because of private property restrictions, and the lower half of Transect 18 was inaccessible.

Model	Stand age (yr)	Minimum temperature (°C)	Maximum temperature (°C)	Precipitation (mm)	*P*-value	Adjusted R^2	AIC
Model 1	–128.9*				0.039	0.13	285.5
Model 2		–132.3*			0.023	0.16	284.5
Model 3	–145.5**	–146.9**			0.003	0.35	278.7

Table 2.5 Multiple regression models examined the relationship between elevational range changes of plethodontid salamanders in the southern Appalachian Mountains and trends in minimum and maximum temperature and precipitation and the forest stand age during Hairston surveys (1949, 1951). Regression coefficients are provided by model. The dependent variable is the change in the lower elevational range limit (m) for the *Plethodon jordani* complex and *Desmognathus organi* and the change in upper elevational range limit (m) for the *P. glutinosus* complex and *P. yonahlossee* on transects (n = 26). Maximum and minimum temperature and precipitation are trends for the 10 years previous to the Hairston and 2011 surveys. Levels of significance for coefficients are as follows: * $P < 0.05$; ** $P < 0.01$. Adjusted R^2, P-values, and Akaike information criterion (AIC) values are given for each model. All models including either maximum temperature or precipitation as independent variables were not significant.

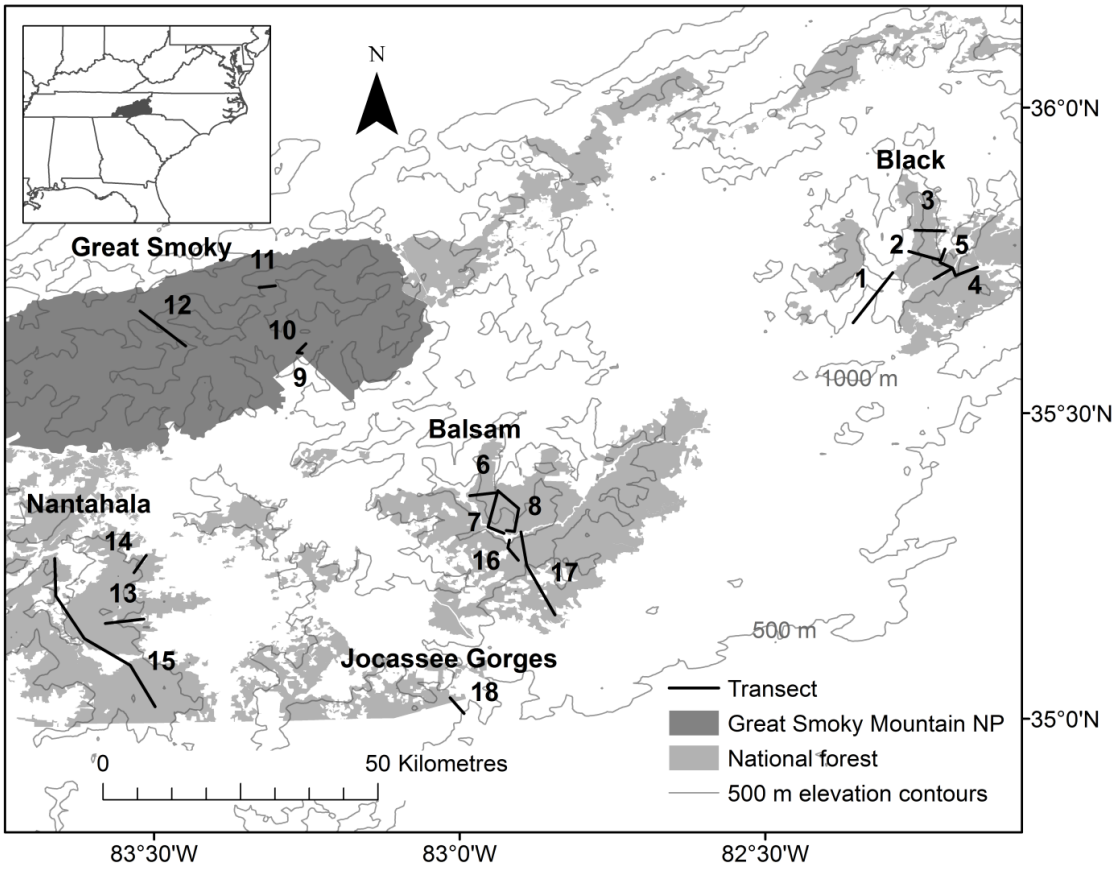

Figure 2.1 Map of the southern Appalachian Mountains showing the 18 transects resurveyed for plethodontid salamanders in the summer of 2011. The numbers follow Hairston (1951), except Transect 4, which is Sugar Cove. Mountain ranges are labelled. The shaded region in the inset shows the study region within the southeastern USA.

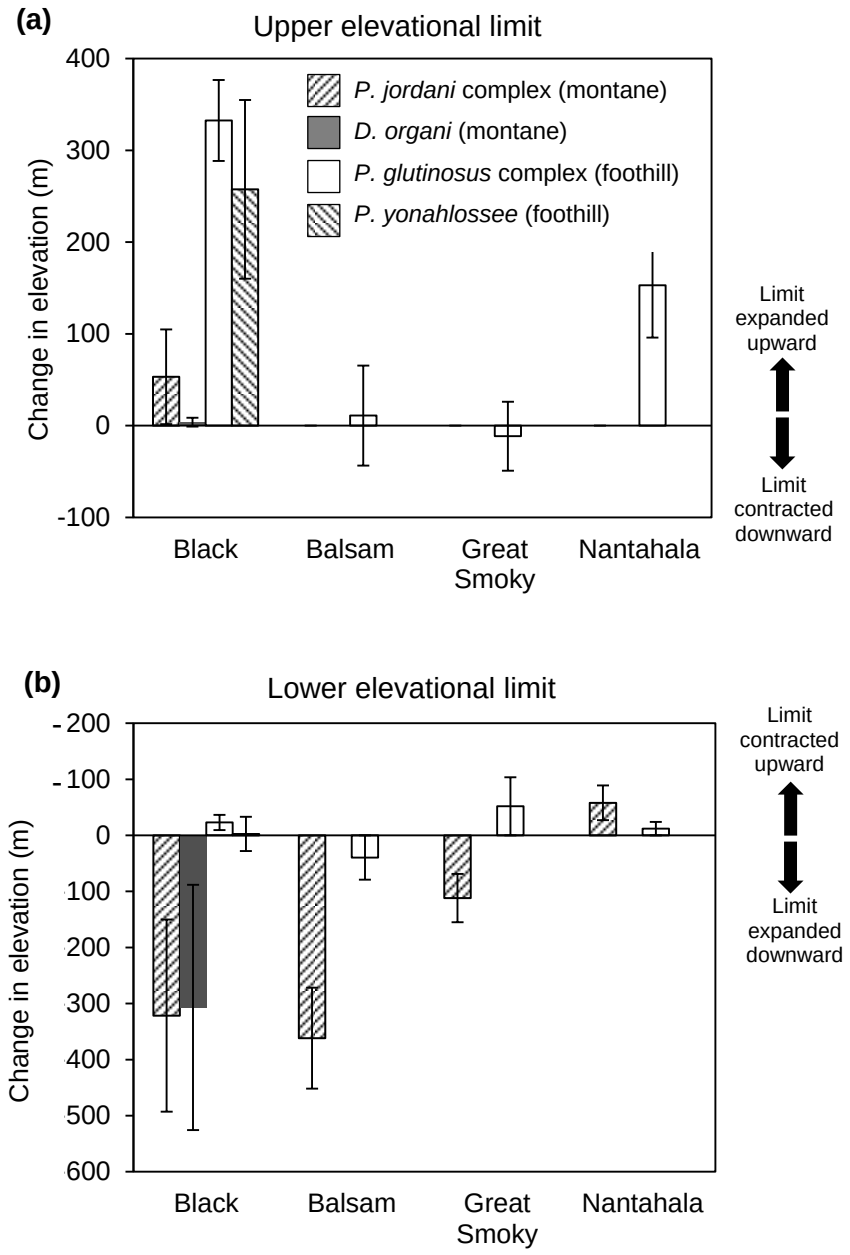

Figure 2.2 Average changes (± one standard error) in the (a) lower and (b) upper elevational range limits for plethodontid salamander species on each mountain range surveyed in the southern Appalachians. The species are categorized as either montane (*Plethodon jordani* complex and *Desmognathus organi*) or foothill (*Plethodon glutinosus* complex and *P. yonahlossee*). Positive values indicate expansions, negative values contractions. Sample sizes are as follows: n = 4 for all species in the Black Mountains, n = 5 for the *Plethodon glutinosus* complex and n = 3 for the *P. jordani* complex in the Balsam Mountains, n = 4 for all species in the Great Smoky Mountains, and n = 3 for all species in the Nantahala Mountains.

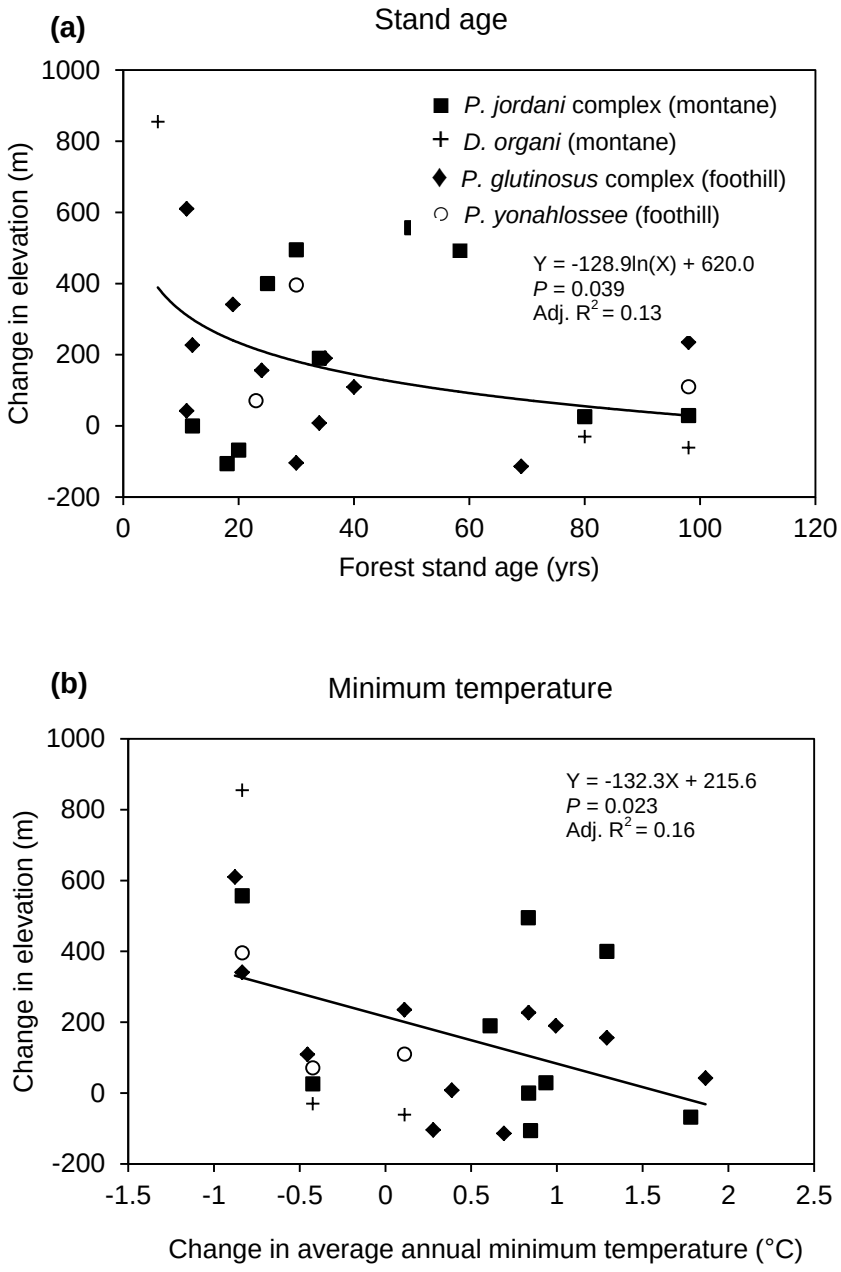

Figure 2.3 Regressions for (a) forest stand age during the Hairston surveys (1949, 1951) and for (b) average annual minimum temperature trends (i.e., changes between the 10 years previous to the Hairston and 2011 surveys) and the elevational range changes of all plethodontid salamander species by transect (n = 26) in the southern Appalachian Mountains. A log-linear model was used for the forest stand age regression. The species are categorized as either montane (*Plethodon jordani* complex and *Desmognathus organi*) or foothill (*Plethodon glutinosus* complex and *P. yonahlossee*).

Chapter 3: Sources of Uncertainty in Biodiversity Projections under a Rapidly Changing Climate

ABSTRACT

Species distribution models are frequently used to examine the potential impacts of future climate change on biodiversity. The projections from these models can be greatly affected by a number of decisions during the model-building process, including selection of the spatial modeling region, environmental variables, statistical modeling method, and general circulation model. In this study I quantified the variation in future climate change projections for each of these four factors by examining 2040-2070 projections for 16 species of Plethodontidae salamanders in the southern Appalachian Mountains. Additionally, evaluation metrics (AUC, Kappa, and TSS) for all levels (i.e., each choice) within each factor were examined. Overall, future projections suggest that habitat may become less suitable for these species by mid-century. However, there was a large amount of variation in projections, with most of that variability accounted for by four factors examined. Additionally, each factor's relative contribution varied by species, and the evaluation metrics did not differ greatly between levels within each factor. Overall, my results demonstrate the need to examine multiple sources of uncertainty and take an ensemble forecasting approach to climate change studies, especially since evaluation metrics do not allow comparison of models or the selection of the 'best' model. My results also suggest that climate change projections should be presented with estimates of uncertainty, so researchers and decision makers can take this into account when making conservation-related decisions. Finally, I believe that additional resources should be invested into understanding the ecological factors that limit species' distributions and how to use that information to construct accurate projection models.

INTRODUCTION

Species distribution models have been widely used to predict the suitability of current habitat (Guisan & Zimmerman, 2000), find new regions occupied by a species (Bourg et al., 2005; Guisan et al., 2006a), discover closely related species (Raxworthy et al., 2003), evaluate the potential for establishment and spread of nonnative species (Higgins et al., 1999; Thuiller et al., 2005a), and examine the potential impact of future climate change (Bakkenes et al., 2002; Erasmus et al., 2002; Peterson et al., 2002; Thuiller et al., 2005b; Araujo et al., 2006). Studies involving climate change use species' presence points and current environmental datasets to build models, which are transferred onto projected future environmental datasets. The outputs from these transferred models can be greatly affected by a number of decisions made during the modeling process, and a growing number studies have investigated the sources of these uncertainties (Araujo & Guisan, 2006; Barry & Elith, 2006; Elith et al., 2006; Guisan et al., 2006b; Heikkinen et al., 2006; Dormann et al., 2008; Graham et al., 2008).

A large part of this investigation has been focused on differences between statistical modeling methods (Araujo et al., 2005; Elith et al., 2006; Pearson et al., 2006). Currently, the research suggests that a method should be chosen based on the data available and the goal of the research (Jimenez-Valverde et al., 2008; Elith & Graham, 2009). However, some have recommended using model-averaging or ensemble methods (Wintle et al., 2003; Thuiller et al., 2003, 2009), as a way to account for the variability between methods, leading to the development of software that can simultaneously run multiple methods (Thuiller et al., 2003, 2009). In addition to between-model variability, some studies have also begun to investigate within-model variability, such as choice of future general circulation model (GCM), environmental predictor variables, and spatial modeling region.

Many studies have examined differences in species distributions projections by using different emission scenarios (Thuiller et al., 2005; Mika et al., 2008; Lawler et al., 2009); however, few have investigated the degree of uncertainty introduced by the choice of GCM (Mika et al., 2008; Durner et al., 2009; Lawler et al., 2009). Different GCMs have been shown to produce widely different predictions of future climates, especially rainfall estimates (Stainforth et al., 2005; Wentz et al., 2007). Additionally, GCMs are coupled with regional climate models (RCM) to generate higher resolution outputs for local regions. Typically, several RCMs are available for a region, thereby compounding the variability in future climate and the species distribution outputs.

Most species distribution models are created using variables derived from temperature and precipitation data. However, there are numerous ways to derive variables from these data, and selection of the variables to include can be difficult. Studies have selected sets of variables based on a variety of criteria including test statistics, such as Akaike's information criterion (Warren & Seifert, 2011; Li et al., 2009), limiting correlations amongst the variables (Kozak & Wiens, 2006; Rodda et al., 2011), expert opinion of the variables that limit a species' range (Kozak & Wiens, 2006; Doswald et al., 2009), and performance in earlier studies (Gregory et al., 2009; Milanovich et al., 2010), or an arbitrary decision may be made. A recent study using 26 different variable sets found that they produced large differences among the future projection maps of *Otis tarda* (great bustard; Synes & Osborne 2011). Despite this finding for a single species, little research has focused on the ways in which the choice of environmental variables affects the results of species distribution models that address climate change.

Finally, when the objective is to extrapolate the results to different geographic regions or time periods, some research has focused on the spatial region chosen to build

models (Anderson & Raza, 2010; Rodda et al., 2011; Rodriguez-Castaneda et al., 2012). Presence-absence or background methods are sensitive to the spatial region chosen, because pseudo-absence points sampled from large spatial regions usually contain more environmental heterogeneity than the same number of points selected from smaller regions. Overall, these studies have found considerable variability in the outputs of transferred models due to choice of spatial extent (Anderson & Raza, 2010; Rodda et al., 2011; Rodriguez-Castaneda et al., 2012), and this aspect of species distribution modeling needs further examination.

Despite many recent papers exploring and attempting to quantify the uncertainty in each of these choices, most have only considered each factor individually. Given that many researchers have limited computational resources, an effort needs to be undertaken to determine which factors contribute the largest percentage of uncertainty to projections of species under climate change. Therefore, this study was designed to examine and quantify the uncertainty of four factors (statistical modeling method, GCM/RCM, environmental variable set, and spatial region) simultaneously for the projections under climate change of 16 species of Plethodontidae salamanders in the southern Appalachian Mountains. Using these four factors, I created a full factorial design and used analysis of variance (ANOVA) to partition the variance by factor for each species. Additionally, I used evaluation metrics, such as area under the curve (AUC), Kappa, and the true skill statistic (TSS), to determine whether certain choices yielded consistently higher scores.

METHODS

Species data

I obtained data for 16 species of Plethodontidae salamanders endemic to the southern Appalachian Mountains from Herpnet (www.herpnet.org) and the Global

Biodiversity Information Facility (GBIF; www.gbif.org) and removed duplicates occurrences (Table 3.1). I also removed presence points with coordinate uncertainties greater than 15 arc-second or occurring outside of the 1971-2000 time period. Fourteen species had over 50 presence points and two had over 25, but fewer than 50 presence points. The ranges of each of these species are contained entirely within the southern Appalachian region of Virginia, Tennessee, North and South Carolina, and Georgia.

Statistical modeling methods

I used 5 statistical modeling methods which are available in BIOMOD 1.1-7.04 (Thuiller et al., 2009), run in R 2.15.1 (R Development Core Team, 2011). Specifically, I used generalized linear models (GLM), multivariate adaptive regression splines (MARS), random forest (RF), generalized boosted models (GBM), and generalized additive models (GAM). I altered the settings of GLM in BIOMOD to incorporate polynomial terms and use AIC for variable selection. Additionally, I set the maximum number of trees to 5000 for GBM. The remaining default settings were unaltered.

Environmental data

Current

For the current time period, I downloaded the PRISM Climate Group's 30 arc-second 1971-2000 average monthly maximum and minimum temperature and precipitation (DiLuzio et al., 2008). Using these data and DIVA-GIS 7.5 (Hijmans et al., 2005), I calculated nineteen bioclimatic variables, commonly used for species distribution models (Table 3.2).

I created subsets of these variables using an automated procedure. Specifically, I created a logistic regression model for each environmental variable, using the presence and pseudo-absence data. Additionally, a Pearson correlation matrix was conducted for

all variables. Using this information, variables were placed into subsets of three, four, or five variables such that they maximized predictive power while constraining correlations between predictors to be less than 0.70 and greater than -0.70. This process was performed without replacement, so that each variable only appeared in a single subset for each species. This procedure usually yielded two to four subsets per species. In addition to the automated procedure, I searched the literature to find sets of variables that previous studies had used to model the distributions of these species (Rissler & Apodaca, 2007; Kozak & Wiens, 2010; Moskwik, 2014). Based on this review, I created three additional subsets for each species (Table 3.2).

Future

I used 11 future climate projections from the North American Regional Climate Change Assessment Program (NARCCAP) for 2041-2070 (Mearns et al., 2009; Table 3.3). One objective of NARCCAP was to investigate the uncertainty of different combinations of GCMs and RCMs over North America. All GCMs were forced with the Special Report on Emission Scenarios (SRES) A2 scenario. The A2 scenario represents a world of independently operating nations, increasing population, and regional economic development (IPCC, 2000). Further, it is one of the higher emissions scenarios and was chosen because current emissions are exceeding this scenario. Additionally, if decision makers can create strategies to mitigate the impacts of this scenario than those strategies should be robust against changes under lower SRES emission scenarios.

Seth McGinnis at the National Center for Atmospheric Research statistically downscaled the climate projections, originally at 50 km resolution, to 30 arc-second using the delta method (Mearns et al., 2001). This method calculates the differences between future climate projections and a historical high resolution dataset, and then applies those

changes to the historical dataset. Seth McGinnis used the 30 arc-second PRISM 1971-2000 monthly average maximum and minimum temperature and precipitation as the historical dataset (DiLuzio et al., 2008). Then I used DIVA-GIS 7.5 (Hijmans et al., 2005) to calculate the 19 future bioclimatic variables. For average annual temperature and precipitation, I calculated the mean change for each over the entire southern Appalachian region (i.e., area encompassing the distributions of all species in this study). Finally, I divided the future bioclimatic variables into subsets that matched the current variable subsets.

Spatial modeling regions

In ArcMap 10.0 (ESRI, 2011) I used the presence points for each species to delineate five different spatial modeling regions. First, I created a conventional convex minimum polygon (MCP). However, this method has been criticized, because it may minimize the environmental contrast between presences and pseudo-absences (Rodda et al., 2011). Thus, for a second spatial region I buffered the MCP by 4 km. The Plethodontidae salamanders in my study are mostly high-elevation species, although a few are low-elevation species, so a 4-km geographic buffer incorporated environmental space from the valley floors for high-elevation species and the high mountain peaks for low-elevation species. Incorporating this additional environmental space in both cases enhanced the environmental contrast between presences and pseudo-absences. Another potential criticism of both the MCP and buffered MCP is that pseudo-absences could be selected from areas within the species range, where the species is present, but there are not presence records (i.e., false absences). To address this issue, I took the buffered MCP and prevented pseudo-absences from being selected within 2-km of presence points.

I also used a local convex hull (LCH) method developed at the University of California, Berkley (Getz & Wilmers, 2004). This method may provide better range estimates when there are 'sharp' boundaries or 'holes' in species ranges due to landscape features, such as valleys or mountains. It works by creating local hulls from the k-1 nearest neighbors of every point and then joins them into a single estimate of the range. I varied the value of k for each species until the algorithm produced an estimate of the range that closely matched the known range. Again, a potential drawback of this method is the environmental contrast between presences and absences, so I also created a 4-km buffered LCH.

Pseudo-absence and training replicates

I partitioned the presence data for each species into 20% 'test' and 80% 'training' data. I used the 'training' data to build the models and the 'test' data for the calculation of evaluation metrics. For each spatial modeling region, I drew 5 different sets of pseudo-absence points randomly from the background. Following the recommendations of Barbet-Massin et al. (2012), I drew the same number of pseudo-absence points as 'training' presence points, unless there were fewer than 100. For that case, I drew 100 pseudo-absence points. For each pseudo-absence replicate, I randomly partitioned the presence data 5 times into 'training' and 'test' data, yielding 5 'training' replicates.

Data analysis

Overall, my full factorial design with 5 total factors (statistical modeling methods, environmental variable subsets, spatial modeling regions, and pseudo-absence and 'training' replicates) yielded between 3,125 and 4,375 models per species. I projected these models onto one spatial modeling region for comparison and analysis for the current time period. Additionally, I projected all models onto 11 future climates (a 6th

factor), which also had the same spatial modeling region. I selected the MCP buffered by 4 km as the spatial modeling region for both present and future projections, since it had the largest geographic extent.

For the present and future projections separately, I conducted a type III ANOVA in R 2.15.1 (R Development Core Team, 2011) for all pixels individually using the suitability scores across all projections. I divided each factor's sums of squares by its respective degrees of freedom, yielding the mean square for each. Finally, I calculated the proportional mean square of each factor by dividing its mean square by the sum of the mean square for all factors. Overall, this yielded the proportional mean square by pixel for every factor. Additionally, for both time periods I calculated the ensemble mean and total variance of suitability by pixel. Then I calculated the means of suitability, variance, and proportional mean square by factor across all pixels in the entire 4 km buffered MCP region for each species and both time periods.

I calculated AUC, Kappa, and TSS evaluation metrics using three different spatial extents. First, for each of the present projections I calculated the metrics by using the withheld 20% 'test' data. Second, I used the 4 km 'buffered MCP' projections and all presence data to calculate the metrics. Finally, for 8 species (Table 3.1) I projected all models onto a second PRISM dataset (DiLuzio et al., 2008) for the time period 1981-2010. To calculate evaluation metrics for these projections, I used an 'independent' presence and absence dataset which was gathered during the summer of 2011 (Moskwik 2014). For each spatial extent and species, I averaged the evaluation metrics for each spatial modeling region, environmental variable subset, and modeling method.

RESULTS

Current and future projections

For most species the average suitability for the 4 km buffered MCP region decreased in future projections, compared to current projections (Figure 3.1). These decreases ranged from 0.02 to 0.17. Exceptions were *Desmognathus marmoratus*, *Plethodon aureoles*, and *Plethodon welleri*, where small increases of approximately 0.04 were projected. The average variance across all projections increased substantially between current and future projections for all 16 species (Figure 3.1), by 1.8 to 4.6 times current projections.

The variability across the projections can be largely explained by 3 of 5 factors for current (Figure A.1) and 4 of 6 for future projections (Figure 3.2). Statistical modeling method, environmental variable subset, and spatial modeling region accounted for a large majority of the variation in current projections. For future projections, GCM/RCM combination, along with these 3 factors, accounted for the majority of the variation. Pseudo-absence and 'training' replicates accounted for little of the variation for both current and future projections.

Projected changes in average annual temperature and precipitation in the southern Appalachian region varied among the climate projections (Figure 3.3): models predicted 1.8° to 3.1° C increases in average annual temperature. Average annual precipitation was predicted to be either slightly lower or almost unchanged by 2040-2070 for a few models. However, the majority of the models projected that average annual precipitation will increase in the region, some by as much as 205 mm.

Evaluation metrics

Despite the large variation in current projections of suitability, the average AUC evaluation scores showed little differences between levels within each factor (i.e., spatial modeling region, environmental variable subset, and statistical modeling method). For the 'test' approach, only the spatial modeling region yielded slightly different AUC scores for each level (Figure A.2). For the 'buffered MCP' approach, small differences between levels were only seen for the statistical modeling method (Figure 3.4), which consistently showed random forest slightly outperforming the other methods. Finally, the 'independent' approach showed no large consistent differences between levels in each factor, although the LCH background had slightly lower scores than other backgrounds (Figure A.3). The average Kappa and TSS evaluation scores showed similar results (Figures A.4, A.5, and A.6).

DISCUSSION

The average decrease in suitability values for future versus current projections for most species suggests that the climate of the southern Appalachian Mountains may be less favorable for Plethodontidae salamanders by mid-century. Less favorable climate could potentially lead to range contractions and/or reduced populations. My results and interpretation are consistent with Milanovich et al. (2010), which projects that Plethodontidae salamanders in this region may undergo large range contractions due to climate change during the 21st century. However, there is a large amount of variation in my future projection outputs, which has also been observed in similar climate change projection studies of other vertebrates (Buisson et al., 2010; Synes & Osborne, 2011).

My results, showing that the spatial modeling region can contribute large amounts of variation to current and future projections, are not surprising given similar findings from other studies (Barve et al., 2011; Acevedo et al., 2012). This variation is due to the

locations of pseudo-absence points used during the model-building process. Ideally, these pseudo-absences would be taken from localities where the species is absent, but accessible by dispersal over 'relevant' periods of time (Barve et al., 2011). However, identifying these regions is difficult, if not impossible, for most species. Thus, most modelers are left estimating these regions, and my results suggest that a single estimation may not be sufficient to account for the uncertainty in climate change projections.

A large amount of research has already been conducted on the variability in projections of species responses to climate change due to statistical modeling method chosen (Thuiller, 2003; Lawler et al., 2006; Pearson et al., 2006; Roura-Pascual et al., 2009). This variability is due to each method's different mathematical algorithms and assumptions, yielding different ecological niche estimates (Buisson et al., 2010). This has led many modelers to conclude that several methods should be used when conducting climate change studies (Thuiller et al., 2003, 2009). My study, which included additional sources of uncertainty, further indicates that the statistical modeling method contributes a large amount of uncertainty to climate change projections, and thus using more than one statistical modeling method should be used.

My results also demonstrate that the selection of environmental variables can greatly affect projections, especially future projections. This may be surprising given that the 21 different variables in my study were derived from monthly averages of maximum and minimum temperature and precipitation; however, it appears that this choice is not arbitrary. Thus, if modelers are unaware of the specific environmental factors that limit a species' distribution, several environmental variable subsets should be created to fully examine and account for the uncertainty in model projections. Additionally, I believe that more research is needed in this area, since few papers have investigated this

potentially significant source of uncertainty in climate change projections (Synes & Osborne, 2011).

In this study GCM/RCM combination was a small, although important contributor to the variation in future projections. I was surprised that the GCM/RCM combination did not account for a larger proportion of the variation in species projections, since the 11 climate models varied considerably. These results suggest that the uncertainty in future species' projections is mostly due to the uncertainty in species' modeling, rather than the uncertainty in the climate change projections. Therefore, modelers can best reduce future uncertainty in species' projections by better understanding the environmental factors that limit species and developing methods that accurately capture that ecology.

Finally, my results demonstrate that both pseudo-absence and 'training' replicates account for little of the total variation in model projections. Thus, to save computational time and space, modelers should consider reducing the number of these replicates in favor of examining other sources of uncertainty, such as those I examined in this study.

Despite the variability in the current and future model outputs, there was relatively little difference in the evaluation metrics (i.e., AUC, Kappa, and TSS) between levels of each factor. The differences between spatial modeling regions in the 'test' approach are due to the metrics being calculated on their respective spatial extents, and thus their values cannot be directly compared. When this factor is examined using the 'buffered MCP' or 'independent' approach, most differences disappear. Surprisingly, the evaluation metrics did not differ between the environmental variable subsets generated by my automated approach versus those selected from the literature. Additionally, except for random forest performing slightly better than the other statistical models under the 'buffered MCP' approach, no large differences were observed. Overall, the evaluation metrics I examined do little to narrow down which model projections may be more

accurate or likely, despite the large observed difference in projections. Better evaluation metrics are needed.

My results demonstrate the need to examine multiple sources of uncertainty and take an ensemble forecasting approach to climate change studies, especially since evaluation metrics do not allow for the selection of the 'best' model. Specifically, more than one spatial modeling region, statistical modeling method, environmental variable subset, and GCM/RCM combination should be examined. Examining uncertainty across these factors may require significant computational time and space. Therefore modelers could consider reducing the number of 'training' or pseudo-absence replicates, since they do not provide relatively large amounts of uncertainty to model projections. My results suggest that climate change projections should be presented with estimates of uncertainty, so researchers and decision makers can take this uncertainty into account when making conservation-related decisions. Finally, to increase the accuracy of species' projections I believe that additional resources should be invested into understanding the environmental factors that limit species' distributions.

TABLES & FIGURES

Species	Code	Transect data
D. carolinensis	DECA	X
D. imitator	DEIM	
D. marmoratus	DEMA	
D. orestes	DEOR	
D. organi	DEORG	X
D. santeetlah	DESA	
D. wright	DEWR	
P. aureoles	PLAU	
P. chattahoochee	PLCH	
P. jordani	PLJO	X
P. metcalfi	PLME	X
P. montanus	PLMO	X
P. shermani	PLSH	X
P. teyahalee	PLTE	X
P. welleri	PLWE	
P. yonahlossee	PLYO	X

Table 3.1 *Desmognathus* and *Plethodon* spp. studied, their coded names, and the use of transect data. Independent presence/absence transect data (Moskwik 2014) were used for evaluation metrics of only 8 of the species.

Environmental variable	Rissler & Apodaca (2007)	Kozak & Wiens (2010)	Moskwik (2014)
Annual mean temperature	X		
Mean diurnal range	X	X	
Isothermality	X		
Temperature seasonality			
Maximum temperature of warmest month		X	
Minimum temperature of coldest month			
Temperature annual range	X		
Mean temperature of wettest quarter	X		
Mean temperature of driest quarter	X		
Mean temperature of warmest quarter			
Mean temperature of coldest quarter			
Annual precipitation			X
Precipitation of wettest month			
Precipitation of driest month			
Precipitation seasonality	X		
Precipitation of wettest quarter	X		
Precipitation of driest quarter	X	X	
Precipitation of warmest quarter	X		
Precipitation of coldest quarter	X		
Average annual maximum temperature			X
Average annual minimum temperature			X

Table 3.2 The environmental variables used in species distribution models. The automated procedure used all environmental variables, except average annual maximum and minimum temperature. Additional subsets were created based on previous studies.

RCM	GCM			
	CCSM	CGCM3	GFDL	HADCM3
CRCM	X	X		
ECPC			X	
HRM3			X	X
MM5I	X			X
RCM3		X	X	
WRFG	X	X		

Table 3.3 The coupled global climate models (GCM) and regional climate models (RCM) used for future projections. Model abbreviations are as follows: Canadian Regional Climate Model (CRCM); Experimental Climate Prediction Center Regional Spectral Model (ECPC); Hadley Regional Model 3 (HRM3); MM5 – PSU (MM5I); Regional Climate Model 3 (RCM3); Weather Research and Forecasting Model (WRFP); Community Climate System Model (CCSM); Third Generation Coupled Global Climate Model (CGCM3); Geophysical Fluid Dynamics Laboratory (GFDL); Hadley Centre Coupled Model 3 (HADCM3).

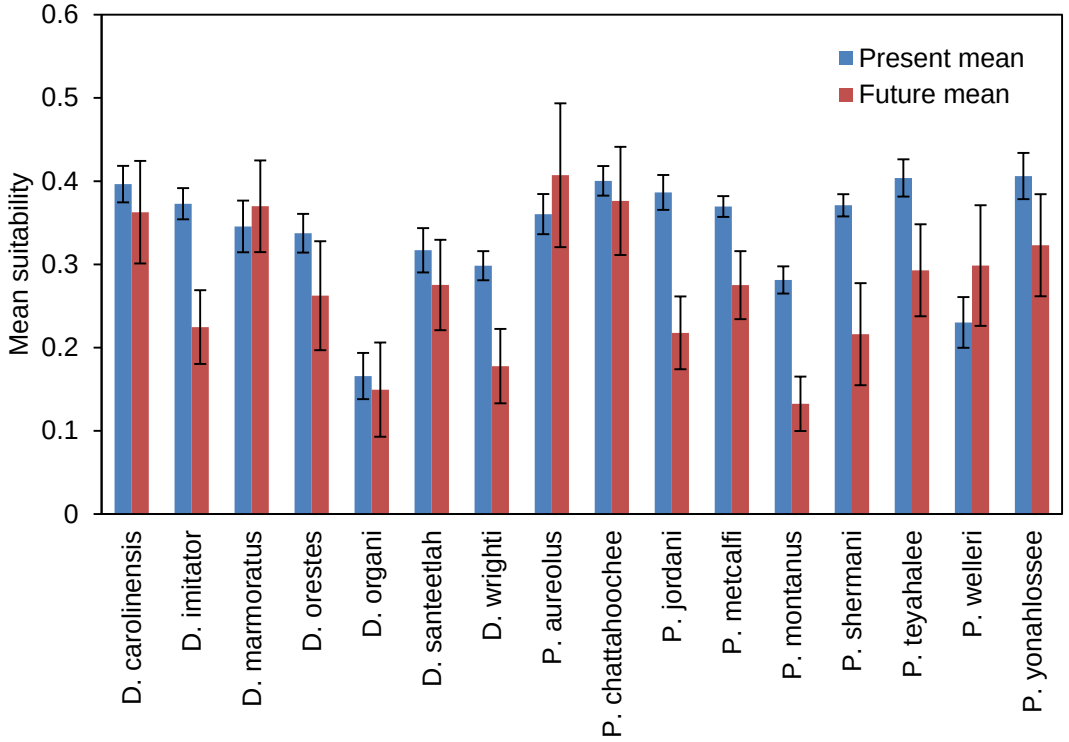

Figure 3.1 Average suitability across each species range, based on 4 km buffered minimum convex polygons, for each of 16 species of Plethodontidae salamanders in the southern Appalachian Mountains. Blue: current (1970-2000) range; red: future (2040-2070) projected ranges. Error bars: represent variance among models.

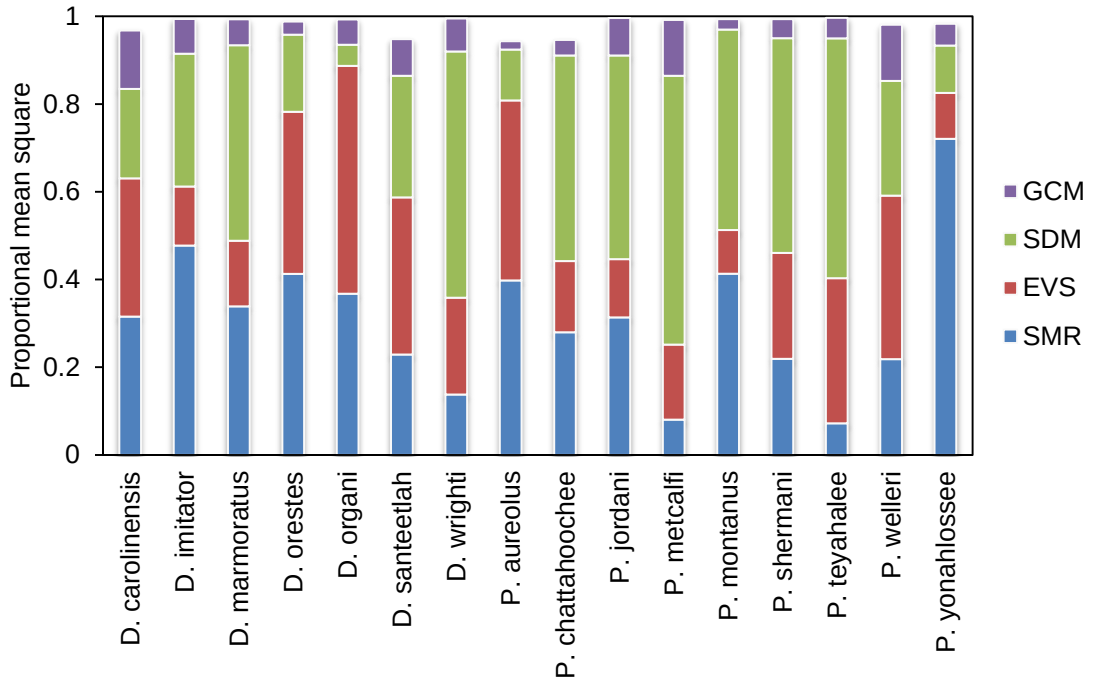

Figure 3.2 Average proportional mean squares of variance attributed to spatial modeling region (SMR), environmental variable subset (EVS), statistical modeling method (SDM), and general and regional circulation model combination (GCM/RCM), for each of 16 species. These variances were calculated from the projected ranges (future projections: 2040-2070). 'Training' and pseud-absence replicates are not displayed; they accounted for only small amounts of variance.

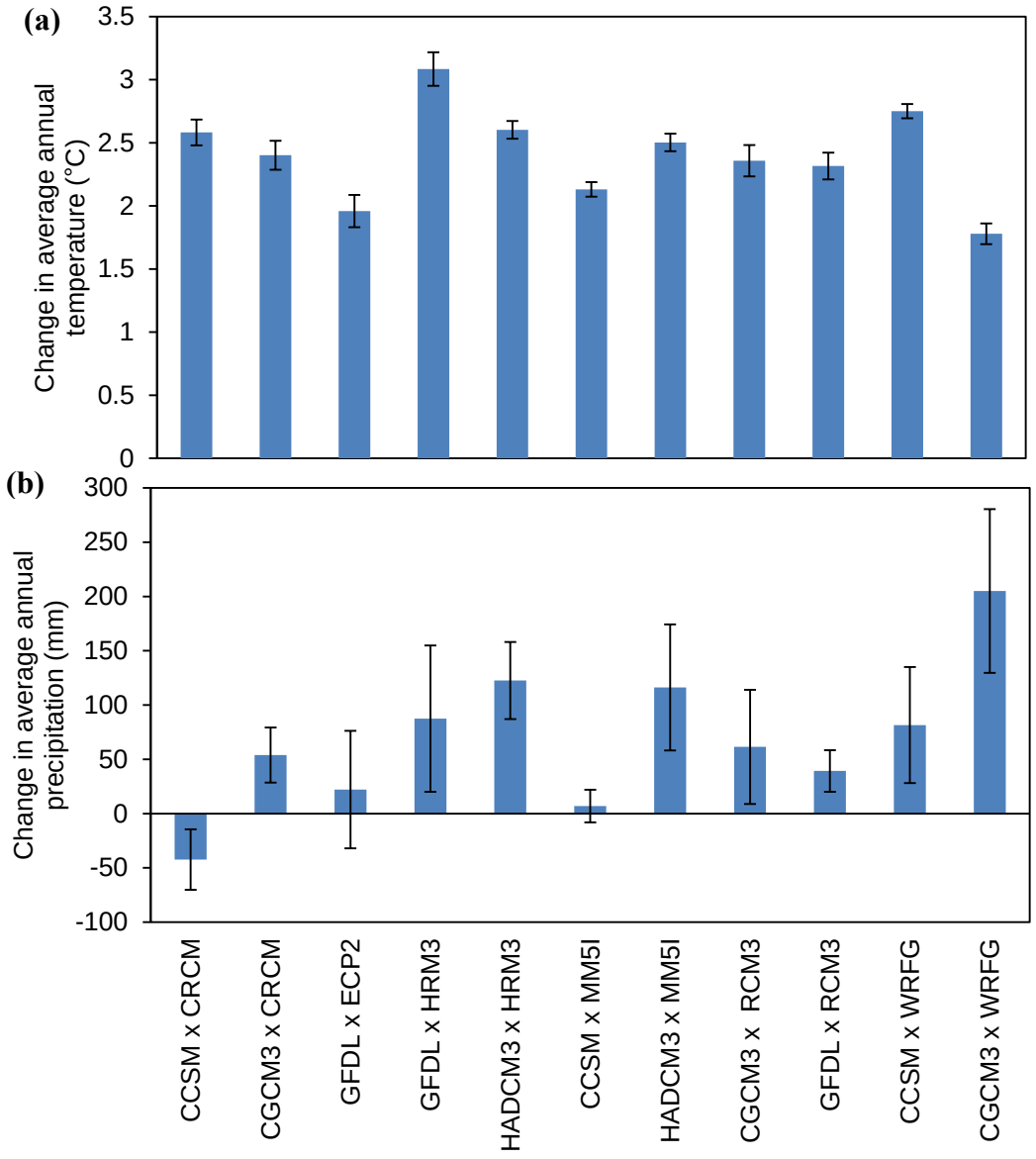

Figure 3.3 Projected changes in average annual (a) temperature and (b) precipitation in the southern Appalachian Mountains from 11 general and regional climate model combinations. Error bars represent standard deviations across all pixels. Model abbreviations are as follows: Canadian Regional Climate Model (CRCM); Experimental Climate Prediction Center Regional Spectral Model (ECPC); Hadley Regional Model 3 (HRM3); MM5 – PSU (MM5I); Regional Climate Model 3 (RCM3); Weather Research and Forecasting Model (WRFP); Community Climate System Model (CCSM); Third Generation Coupled Global Climate Model (CGCM3); Geophysical Fluid Dynamics Laboratory (GFDL); Hadley Centre Coupled Model 3 (HADCM3).

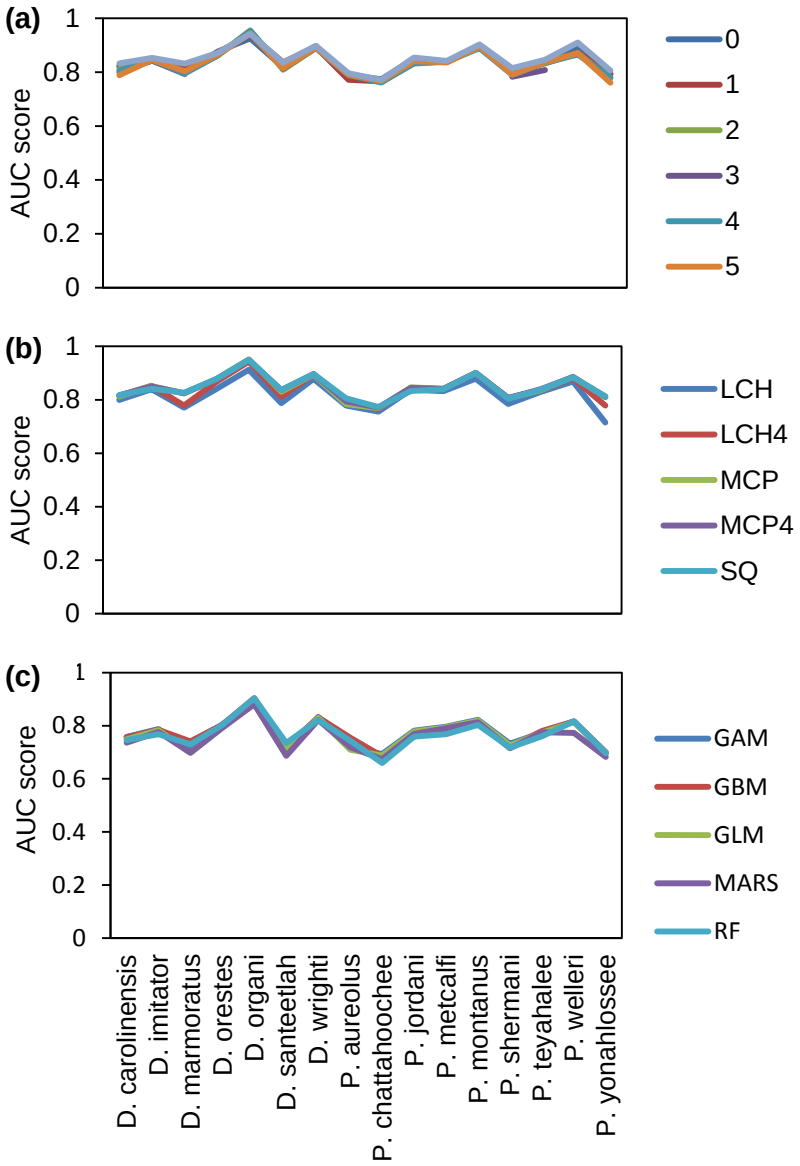

Figure 3.4 The average area under the curve (AUC) scores for each level in (a) environmental variable subset, (b) spatial modeling region, and (c) statistical modeling method are provided. AUC values were calculated on the 4 km buffered minimum convex polygon (MCP4) background. Environmental variable subsets 0-3 were created by an automated procedure and subsets 4-6 were selected from the literature. Models were built on the following backgrounds: local convex hull (LCH), LCH buffered by 4 km (LCH4), minimum convex polygon (MCP), MCP4, and MCP4 excluding 2km around presence points (SQ). For the statistical modeling method the algorithms were generalized additive models (GAM), generalized boosted models (GBM), generalized linear models (GLM), multivariate adaptive regression splines (MARS), and random forest (RF).

Chapter 4: Shifting biodiversity hotspots in the southwestern United States due to projected climate change

ABSTRACT

Recent climate change has already caused range shifts for many species, and future changes in the climate will likely lead to additional large-scale changes in species assemblages and richness. Species distribution models have been used to project changes to species' ranges, however recent studies have indicated that models are highly sensitive to many of the choices by modelers. In this study I examine the potential impacts of future climate change on 164 species endemic to a five state region in the southwestern United States by 2041-2070 and incorporate several sources of uncertainty into model projections. The results indicate several regions in California, southern Oregon, and northern Arizona which will continue to harbor a large number of species. These regions should receive extra attention and protection from conservationists and land managers. Additionally, my results suggest that by mid-century, large range declines may occur for some species, unless they are able to migrate large distances. Conservationists and land managers should consider a variety of conservation strategies including increasing habitat connectivity, protecting habitat outside current ranges, human-assisted colonization, and habitat engineering to help species move with rapidly shifting climates through a fragmented landscape.

INTRODUCTION

Recent global climate change has already affected ecosystems and led to range shifts of many species (Parmesan & Yohe, 2003; Root et al., 2003; Parmesan, 2006). Future projected climate change has the potential to further alter species' distributions, potentially leading to large-scale changes in species assemblages and richness for some regions (Warren et al., 2013). An important tool that has been employed to examine

these potential future changes is species distribution models, which have suggested that some regions may experience high levels of species loss during the 21st century (Peterson et al., 2002; Araújo et al., 2004; Thuiller et al., 2005).

However, only a few of these efforts have incorporated multiple sources of uncertainty into their estimates, despite an overwhelming amount of evidence that projections are highly sensitive to model settings or choices by the modeler (Araújo et al., 2006; Barry & Elith, 2006; Guisan et al., 2006b; Dormann et al., 2008; Graham et al., 2008; Elith & Graham, 2009; Warren et al., 2014). For example, the results in Chapter 3 showed that the choice of modeling region, environmental variables, species distribution model, and future climate change projection can greatly affect the model outputs of future climate change projections of Plethodontidae salamanders in the southern Appalachian Mountains. Therefore, any effort to assess future changes in species richness or assemblage should incorporate such sources of uncertainty into model projections.

The climate of the southwestern United States has changed over the last century with an average annual temperature increase of 0.8° C and decreased average mountain snowpack (Karl et al., 2009). By mid-century the temperature is projected to rise an additional 1.4° to 3.1° C, droughts are expected to become more frequent and severe (Karl et al., 2009), and the monsoon season, which is critical for some species, may be dramatically altered (Asmerom et al., 2013). These changes will likely impact many species endemic to the region, including those in the California Floristic Province, an internationally important and recognized biodiversity hotspot. Therefore, an effort should to be undertaken to quantify the possible impacts of future climate change on these species, so mitigating strategies can be developed if necessary.

A few efforts have been undertaken for birds (Stralberg et al., 2009; Wiens et al., 2009; Jongsomjit et al., 2013) and plants in California (Loarie et al., 2008; Franklin et al.,

2013; Riordan & Rundel, 2014). Overall, these studies project declines in the ranges of bird and plant species later this century; however, they did not examine more than two sources of uncertainty in model projections, limiting the robustness of the results. Additionally, the results were restricted to a single taxonomic group, which limits the identification of specific locations that will harbor biodiversity across multiple taxonomic groups.

In an effort to examine changes in species assemblages and richness in the southwestern United States, I project the current and future distributions of 164 species across multiple taxonomic groups endemic to the region. My species distribution models also incorporate several sources of uncertainty. Specifically, I conducted an analysis similar to that in Chapter 3 on a representative subset of species to determine which sources of variation should be included in all models. After incorporating these sources into my models, I project all species to two separate geographic extents for both current and future time periods. First, I examine and compare species distributions for the current and future time periods at a 'realized' extent, where I assume limited future migration. Second, I conduct the same comparison at a 'potential' extent, where I project all species to the entire southwestern United States for both time periods. This second comparison allows me to examine changes in suitable climate space and assumes unlimited future migration for species.

METHODS

Species data

My study region, which I will refer to as the Southwest, was composed of the following five states: Oregon, California, Nevada, Utah, and Arizona. These states were chosen because data were readily accessible. Data for approximately 1252 species were

obtained from the Natureserve database (Natureserve, 2013). Of these, I only kept species which were endemic to the Southwest, because I wanted my models to include all climate conditions in which the species exists. I removed all presence points with coordinate uncertainties greater than 15 arc-second or occurring outside of the 1971-2000 time period. Then I removed species with fewer than 15 presence points, so as to reduce errors associated with small sample sizes (Stockwell & Peterson, 2002). Additionally, I removed fully aquatic or saltmarsh species, because additional environmental covariates, such as flow and sea-level rise, which I did not incorporate into my models, are probably of primary importance in determining the distributions of those species. Finally, I removed species that currently or historically occurred in the Central Valley of California. Large-scale habitat modification due to agriculture has occurred in the Central Valley and has probably led to range declines for many species. As a result the absence of many species may be a consequence of lack of suitable habitat, not climate, and so it is likely that the resulting models would not accurately depict the suitable climate space for these species. Overall, this yielded 164 species for the analysis.

Current climate data

For the current time period, I downloaded the PRISM Climate Group's 30 arc-second 1971-2000 average monthly maximum and minimum temperature and precipitation grids (Di Luzio et al., 2008). In DIVA-GIS 7.5 (Hijmans et al., 2005), I calculated nineteen bioclimatic variables, commonly used for species distribution models, from these data (Table 4.1). I separated the bioclimatic variables into two to four subsets per species based on rule-based criteria outlined in Chapter 3. Specifically, using presence and pseudo-absence points I conducted a logistic regression for each variable individually. Additionally, a Pearson correlation matrix was conducted for all variables.

Using this information, variables were placed into subsets of three, four, or five variables such that they maximized predictive power while constraining correlations between predictors to be less than 0.70 and greater than -0.70. This process was performed without replacement, so that each variable only appeared in a single subset for each species. I downloaded the 2010 Census Urban Area layer (US Census Bureau, 2010), and used it to remove urban areas from the bioclimatic variables used to build the models. Urban areas were removed so that I did not use pseudo-absence data from regions where climate may be suitable for a species, but the species is not present due to lack of appropriate habitat.

Future climate data

I used 11 future climate projections for 2041-2070 from the North American Regional Climate Change Assessment Program (NARCCAP; Table 4.2) (Mearns et al., 2009). All climate models were forced with the Special Report on Emission Scenarios (SRES) A2 scenario. The A2 scenario was chosen, because it is a high emissions scenario and current emissions are exceeding it. Additionally, Seth McGinnis at the National Center for Atmospheric Research statistically downscaled these data to 30 arc-second using the delta method (Mearns et al., 2001). This method calculates the differences between future climate projections and a historical dataset, which is typically at a higher resolution. Then any differences are applied to the historical dataset, yielding a higher resolution future projection. Seth McGinnis used the 30 arc-second PRISM 1971-2000 monthly average maximum and minimum temperature and precipitation as the historical dataset, since it was also used for current climate data (Di Luzio et al., 2008). Finally, I used DIVA-GIS 7.5 (Hijmans et al., 2005) to calculate the 19 future bioclimatic

variables. These 19 future variables were separated into subsets to match the current climate data subsets.

Spatial modeling region

A spatial modeling region should include regions where the species is currently present, as well as regions where the species is absent, but has the ability to migrate into during 'relevant' time periods (Barve et al., 2011). Unfortunately, for most species biologists don't have a good understanding of the dispersal capabilities, and thus are unable to delineate an appropriate spatial modeling region (Anderson & Raza, 2010; Barve et al., 2011). Additionally, recent studies have indicated that the spatial modeling region used to build models may affect climate change projections (Anderson & Raza, 2010; Rodda et al., 2011; Rodríguez-Castañeda et al., 2012).

Due to this uncertainty, I elected to use four different spatial modeling regions. I used a minimum convex polygon buffered by 10km and 25km to provide models using different assumptions about the dispersal capabilities of species. One drawback of these regions is that pseudo-absences could be selected from areas within the species range where the species is present, but where there are not presence records (i.e., false absences). To address this issue, I constructed a separate set of background regions from these minimum convex polygons by removing all grid cells within 2-km of presence points.

Species distribution modeling method

I employed BIOMOD 1.1-7.04 (Thuiller et al., 2009) in R 2.15.1 (R Development Core Team, 2011) for the species distribution models. I built models using generalized linear models (GLM), multivariate adaptive regression splines (MARS), random forest (RF), and generalized boosted models (GBM). I altered the settings of GLM to

incorporate polynomial terms and utilize AIC for model selection. Additionally, I changed the maximum number of trees for GBM to 5000. The remaining default settings were unaltered. All models were run on the Texas Advanced Computing Center's Lonestar machine (The University of Texas at Austin).

Training and pseudo-absence replicates

For each species I randomly selected 500 pseudo-absence points from each of the four spatial modeling regions. This was repeated four additional times, yielding five pseudo-absence replicates per species. Then for each of these replicates, I randomly divided the presence data five times into 80% 'training' and 20% 'testing' data, yielding 5 'training' replicates per pseudo-absence replicate.

ANOVA

Due to the time and computational resources required for ANOVA, I selected 22 of the 164 species (Table A.4). This subset consisted of species from a variety of taxonomic groups, from different geographic regions, and of varying range sizes. For each species I examined the variance in future projections due to 6 factors. I conducted a full factorial design using 4 spatial modeling regions, 2 to 4 environmental variable subsets, 4 species distribution models, 11 future climate projections, 5 pseudo-absence replicates, and 5 'training' replicates to create between 8800 and 17600 models per species. Each of these models was projected onto the minimum convex polygon for that species buffered by 25 km. I conducted a type III ANOVA in R 2.15.1 (R Development Core Team, 2011) for all pixels individually using the suitability scores across all projections. For each factor I divided its sum of squares by its degrees of freedom, yielding mean square for each. Finally, I calculated the proportional mean square of each factor by dividing its mean square by the total mean square across all factors. Overall,

this yielded the proportional mean square by factor for each pixel. To summarize across the entire spatial modeling region, I calculated the means of each factor across all pixels.

Analysis for all 164 species

Based on the results of the ANOVA conducted here and in Chapter 3, I find that very little of the uncertainty in suitability was due to differences between pseudo-absence or 'training' replicates. As a result, I decided to only include one pseudo-absence and 'training' replicate for each combination of the remaining 4 factors. This reduced the total number of models per species to between 352 and 704. Every model was projected onto current and future minimum convex polygons buffered by 25 km, with urban areas removed. I will refer to these projections as the 'realized' ranges of species, because they approximate the currently occupied geographic range. Additionally, the future projections assume limited future migration (i.e., less than 25 km from current range boundaries).

In addition to 'realized' extents, all models were projected for both time periods onto the entire Southwest region (i.e., Oregon, California, Nevada, Utah, and Arizona). I will refer to these projections as 'potential' ranges, because they represent the 'potential' geographic range that is climatically suitable for a species. Since I was interested in all regions that had suitable climate space, urban areas were not removed from both current and future projections.

Area Under the Curve (AUC) scores were calculated for each model using two spatial extents. First, I calculated it using the 20% 'test' data on the spatial modeling region used to build the model. However, AUC scores are not comparable across different spatial extents, so I also calculated it for all models using all presence data and the minimum convex polygon buffered by 25 km. This created a standard background

for each species that allowed for comparison across all models. For both backgrounds, scores were averaged across all models. Any species with an AUC score below 0.70 for the latter background was removed from the analysis.

Suitability scores for pixels across all projections were also converted to binary values. One indicated a presence, whereas zero indicated an absence for a pixel. Suitability score thresholds used for the conversion were calculated in BIOMOD (Thuiller et al., 2009) by using a built-in setting, which maximized a model's accuracy according to Receiver Operating Characteristic (ROC).

I created species richness and change maps to determine regions of high biodiversity in the current and future time periods. For each time period and geographic extent I calculated the frequency of presences across all models by pixel for each species. To obtain richness maps, I summed the frequency data for all 164 species. I also calculated 90% confidence interval maps for both time periods and geographic extents. Finally, current maps were subtracted from future maps to obtain species richness change estimates.

To assess changes to the 'realized' and 'potential' ranges of species in the future, I used two metrics: species turnover and range change. The range change metric divided the number of pixels projected to be occupied in the future by the number projected as occupied in the current time period. Thus, overall reductions in a species' range within a geographic extent would yield a fraction below one, while increases will receive values greater than one. The species turnover metric summed the number of pixels projected to be currently occupied that were also projected to be occupied in the future and divided by the total number of pixels projected to be occupied in the future. Outputs for this metric ranged between zero and one. Values of one indicate that the entire projected future

range is currently occupied, whereas values of zero indicate that none of it is currently occupied.

Range size change and turnover metrics were calculated for all models of a species. This generated a distribution for both metrics for every species. To assess changes across all species, I obtained the medians for both metrics and combined each, respectively, for all species to create range change and turnover distributions. I also calculated the 90% confidence intervals from individual species distributions.

RESULTS

ANOVA

ANOVA results for the 22 species that I examined indicated that only 4 of the 6 factors examined contribute to most of the variation in future projections (Figure 4.1). Very little of the total variation in projections is attributed to the 'training' and pseudo-absence replicates. For most species, the choice of species distribution model and environmental variable subset contributed the most, ranging collectively from 56% to 99%. The spatial modeling region and future climate projection accounted for the remaining variation.

AUC statistics

For the 'test' approach 148 species had AUC values at or above 0.70, and 67% of those species had values above 0.79 (Table A.4). Using the minimum convex polygon buffered by 25 km and all presence data, all but three species had AUC values above 0.80 (Table A.4). Those three remaining species had AUC values above 0.70, thus no species were removed from the analysis.

'Realized' geographical extent

At the 'realized' geographical extent, the ranges of most species are projected to decline by 2041-2070 (Figure 4.2a). Specifically, 130 species are projected to decline, with 31 of these species declining by more than 90%. The remaining 34 species are projected to increase slightly. In addition to these projected changes in overall range size, turnover is projected to be high (Figure 4.2b). The proportion of the projected future range that is currently occupied is less than 50% for 143 species. For only 7 species is this estimate above 70%. Of these 7 species, 4 are projected to decline by more than 90% in overall size, suggesting that the ranges for these species will all but disappear by 2041-2070, despite low turnover.

However, the confidence intervals for both metrics are large for most species (Table A.5), indicating that there is a high degree of uncertainty in these estimates. Specifically, the lower confidence intervals for 155 species indicate the loss of more than 90% of their current 'realized' range by mid-century. In contrast, suitable climate space for 159 species expands at their upper confidence intervals. Despite the expansions at upper confidence intervals, turnover is still high for the majority of species. Specifically, for 48 species less than 70% of their current 'realized' range will be climatically suitable by mid-century.

Despite large estimates of range declines and high levels of turnover, the species richness maps at the 'realized' extent suggest that regions of high species richness today will continue to harbor large numbers of species into mid-century (Figures 4.3a and b), with some modest losses and gains (Figure 4.3c). Confidence interval maps show little differences from the average map (Figure A.7).

‘Potential’ geographic extent

The ‘potential’ ranges of 99 species are projected to decline, although only 7 are projected to decline by more than 70% (Figure 4.4a). The ‘potential’ ranges of the remaining 65 species may increase slightly, with 4 more than doubling in size. Even though projected declines are lower for ‘potential’ versus ‘realized’ ranges, turnover for the former is still high (Figure 4.4b). Specifically, less than 50% of the future ‘potential’ ranges of 120 species are currently occupied. This estimate is only greater than 70% for 12 species. Overall, this suggests that most of the ‘potential’ ranges of species will shift by 2041-2070, regardless of whether they increase or decrease in size.

Similar to the ‘realized’ projections, the 90% confidence intervals for both metrics at the ‘potential’ geographical extent are large for most species (Table A.5). For the lower confidence interval, the ‘potential’ ranges of 151 species will decline by more than half. Turnover is also projected to be high for all 164 species (i.e., less than 40% of the future range is currently occupied). In contrast, the upper confidence intervals indicate the expansion of ‘potential’ ranges and relatively low turnover (i.e., more than 60% of the future range is currently occupied) for all 164 species.

The species richness maps show both declines and expansions of suitable climate space for many species by mid-century (Figure 4.5). Additionally, confidence intervals maps are not greatly different from the average map (Figure A.8).

DISCUSSION

Overall, I found strong evidence for declines in the ‘realized’ ranges of species by 2041-2070, except at the upper 90% confidence interval. However, at the ‘potential’ geographical extent suitable climate space will continue to exist for the majority of species. This second conclusion is further supported by my results at both low and high confidence intervals, despite some declines at the low confidence interval. Despite

available climate space for most species at the 'potential' geographical extent, turnover is projected to be high. The only exception is the upper confidence interval at the 'potential' geographical extent.

My results showing large declines for species at the 'realized' geographical extent are supported by previous modeling studies in the region (Loarie et al., 2008; Stralberg et al., 2009; Wiens et al., 2009; Franklin et al., 2013; Jongsomjit et al., 2013; Riordan & Rundel, 2014). However, my results indicating that 'potential' climate space will be available for most species has not been explicitly examined in previous studies. Access to this suitable climate space will require species to move rapidly, as suggested by the high levels of turnover in this study. Unfortunately, fragmented landscapes, urban growth, and rapid rates of climate change may make it more difficult for species geographic ranges to track suitable climatic conditions. Thus, several conservation strategies that have previously been suggested could help species reach suitable climate space, specifically increasing habitat connectivity, protecting habitat outside current ranges, human-assisted colonization (Hunter, 2007; McLachlan et al., 2007; Hoegh-Guldberg et al., 2008), and habitat engineering.

Creating habitat corridors between currently protected patches of habitat will be critical for some species, because corridors will allow them to follow shifting climates in space and time (Evans et al., in revision). There are already efforts underway in California to incorporate corridors into conservation and management plans.

For some species, corridors may not be sufficient, because geographic areas with suitable climatic conditions will move outside of currently protected areas. Thus, I recommend that conservationists and land managers compare current and future projections of species to ascertain whether new regions should be protected for species. In my study the species richness and change maps identify the California coast, Sierra

Nevada Mountains, southern California, the Klamath Basin of Oregon, and parts of northern Arizona as 'hotspots' of biodiversity today and into the mid-21st century for the species in this study. These regions should receive additional protection from land managers and conservationists.

Human-assisted colonization might be appropriate if the majority of the 'realized' range disappears, and the species are unable to disperse to suitable future climate space (Hunter, 2007; McLachlan et al., 2007; Hoegh-Guldberg et al., 2008). This could be the result of poor dispersal ability, the lack of appropriate habitat to migrate thru, or the nearest suitable climatic space being located a significant distance from the current range. Additionally, a candidate species would need enough suitable climate space in both time periods, so viable populations of the species could become established today and persist as the climate changes. Several additional criteria would also need to be considered before an introduction was attempted, such as whether other critical abiotic and biotic factors necessary for survival and growth of populations were available, as well as consideration given to impacts on the local community (McLachlan et al., 2007; Hoegh-Guldberg et al., 2008).

Finally, habitat engineering, a highly controversial strategy, may be necessary for some species which lose their entire 'realized' range and the entire 'potential' range lacks the biotic and abiotic factors necessary for survival and reproduction (Evans et al., in revision). In this case, conservationists and land managers may need to alter the habitat by adding or removing factors to guarantee species persistence.

Studies using species distribution models, including mine, are subject to several assumptions, including but not limited to the ability of the models to accurately estimate the climatic niches of species. This assumption is likely violated for many of the species, because presence data is only available for the realized niche (Dormann, 2007; Soberón,

2007; Jiménez-Valverde et al., 2008). This is usually a subset of the species' actual climatic tolerances because there are usually additional factors, such as biotic interactions and unaccounted abiotic factors that limit a species from inhabiting its entire climatic niche (Dormann, 2007; Soberón, 2007; Jiménez-Valverde et al., 2008). Thus, the projections from models probably do not represent the full range of climatic conditions that a species can actually tolerate. Additionally, the models are not able to take into account whether species are able to adapt by behavioral or physiological means or evolve to tolerate changes in the climate (Dormann, 2007).

Despite these limitations, future projections do provide some basic information about the direction and magnitude of change expected for species, as well as regions that may continue to harbor large numbers of species in the future. My results indicate that the 'hotspots' exist along the California coast, Sierra Nevada Mountains, southern California, northern Arizona, and the Klamath region of Oregon. These regions should receive high-priority for protection. Additionally, my results suggest that by mid-century, large range declines or extinctions may occur for some species, unless they are able to move large distances. Thus, conservationists and land managers may want to begin to monitor species and implement species-appropriate conservation strategies if they begin to decline in response to climate change.

TABLES & FIGURES

Environmental variable
Annual mean temperature
Mean diurnal range
Isothermality
Temperature seasonality
Maximum temperature of warmest month
Minimum temperature of coldest month
Temperature annual range
Mean temperature of wettest quarter
Mean temperature of driest quarter
Mean temperature of warmest quarter
Mean temperature of coldest quarter
Annual precipitation
Precipitation of wettest month
Precipitation of driest month
Precipitation seasonality
Precipitation of wettest quarter
Precipitation of driest quarter
Precipitation of warmest quarter
Precipitation of coldest quarter

Table 4.1 The environmental variables used in species distribution models.

GCM	RCM			
	CCSM	CGCM3	GFDL	HADCM3
CRCM	X	X		
EPC2			X	
HRM3			X	X
MM5I	X			X
RCM3		X	X	
WRFG	X	X		

Table 4.2 The coupled general climate models (GCM) and regional climate models (RCM) used for future projections. Model abbreviations are as follows: Canadian Regional Climate Model (CRCM); Experimental Climate Prediction Center Regional Spectral Model (ECPC); Hadley Regional Model 3 (HRM3); MM5 – PSU (MM5I); Regional Climate Model 3 (RCM3); Weather Research and Forecasting Model (WRFP); Community Climate System Model (CCSM); Third Generation Coupled Global Climate Model (CGCM3); Geophysical Fluid Dynamics Laboratory (GFDL); Hadley Centre Coupled Model 3 (HADCM3).

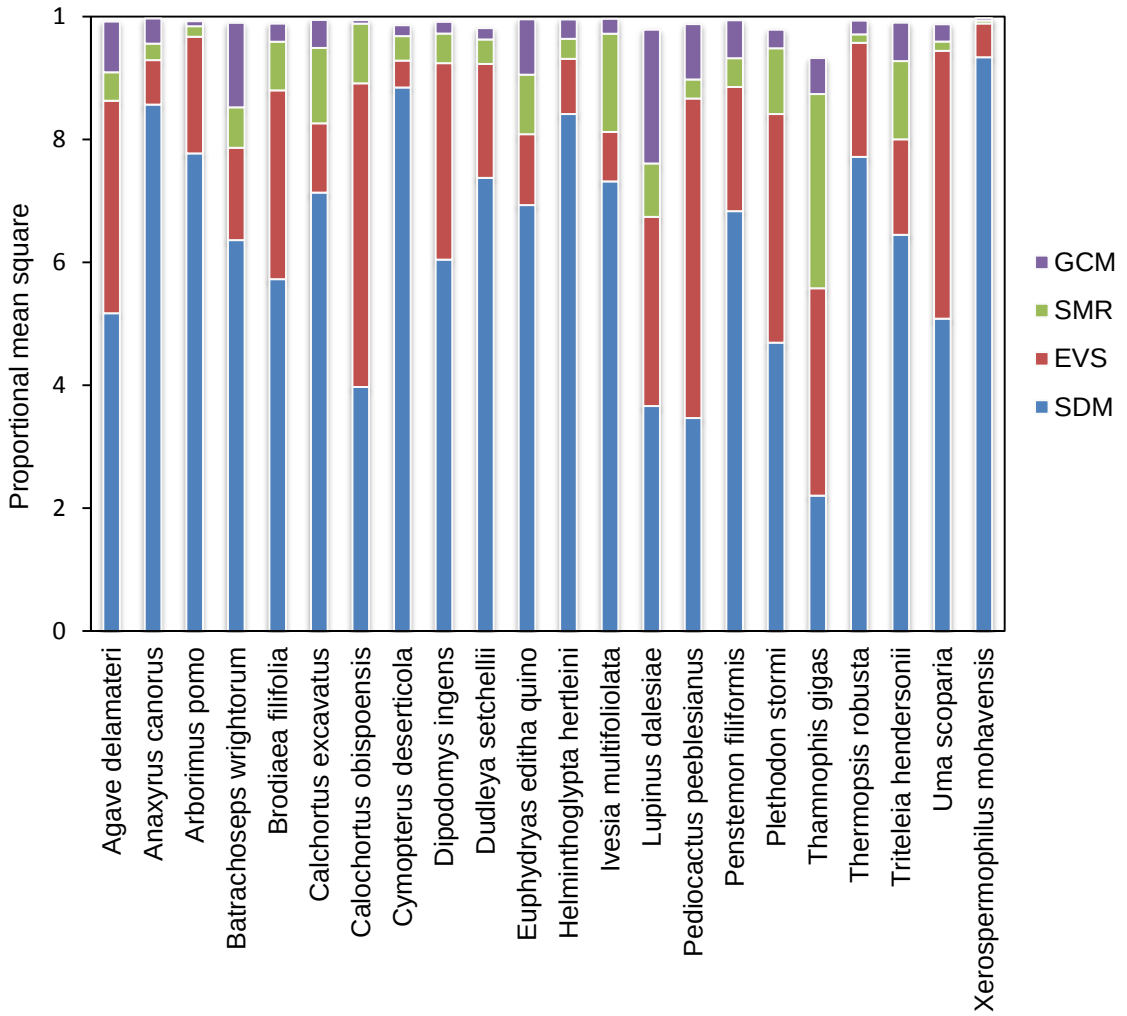

Figure 4.1 The average proportional mean square for species distribution model (SDM), environmental variable subset (EVS), spatial modeling region (SMR), and general and regional circulation model combination (GCM) provided by species for future projections (2041-2070). 'Training' and pseud-absence replicates are not displayed, however account for the remaining proportional mean square.

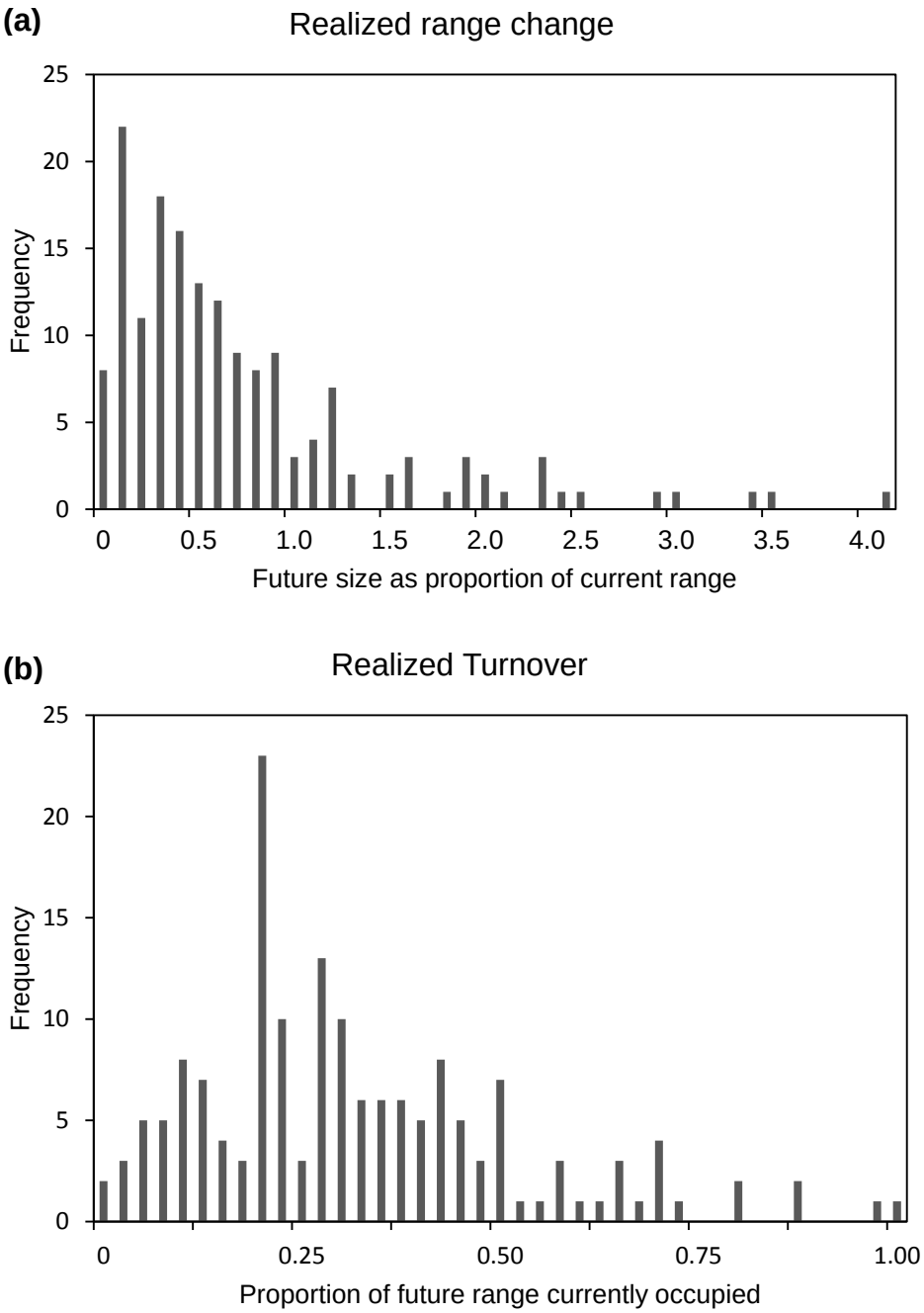

Figure 4.2 Projected A) range change and B) turnover for the 'realized' ranges of 164 species endemic to the southwestern United States. I assume limited future migration of 25 km from current range boundaries. Range change values are obtained by dividing the number of pixels projected to be occupied in the future by those in the present. Turnover is the proportion of the future range that is currently occupied.

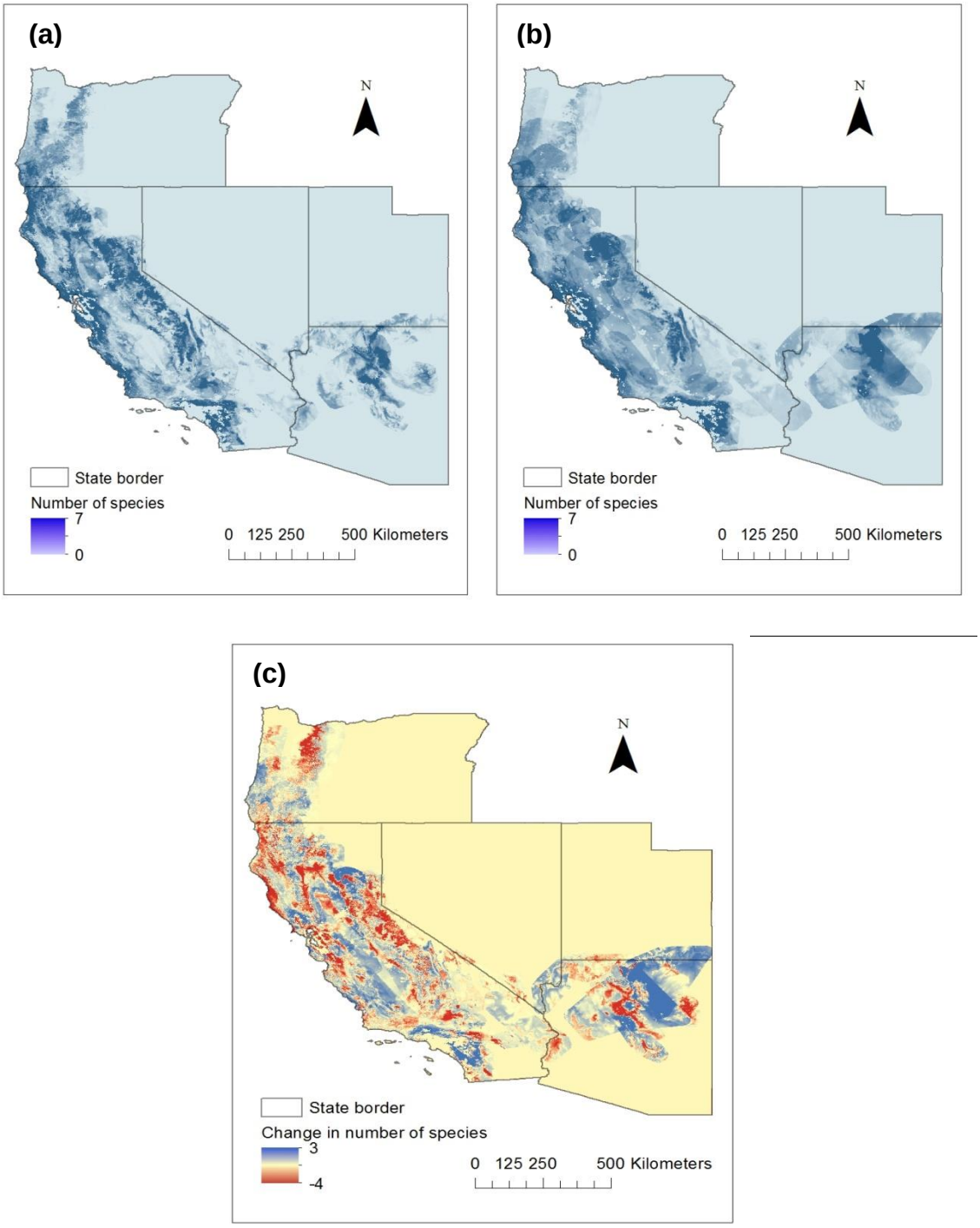

Figure 4.3 Estimates for the 'realized' ranges of A) current, B) future, and C) changes in 164 species endemic to the southwest United States. Future projections assume limited migration of 25 km from current range boundaries.

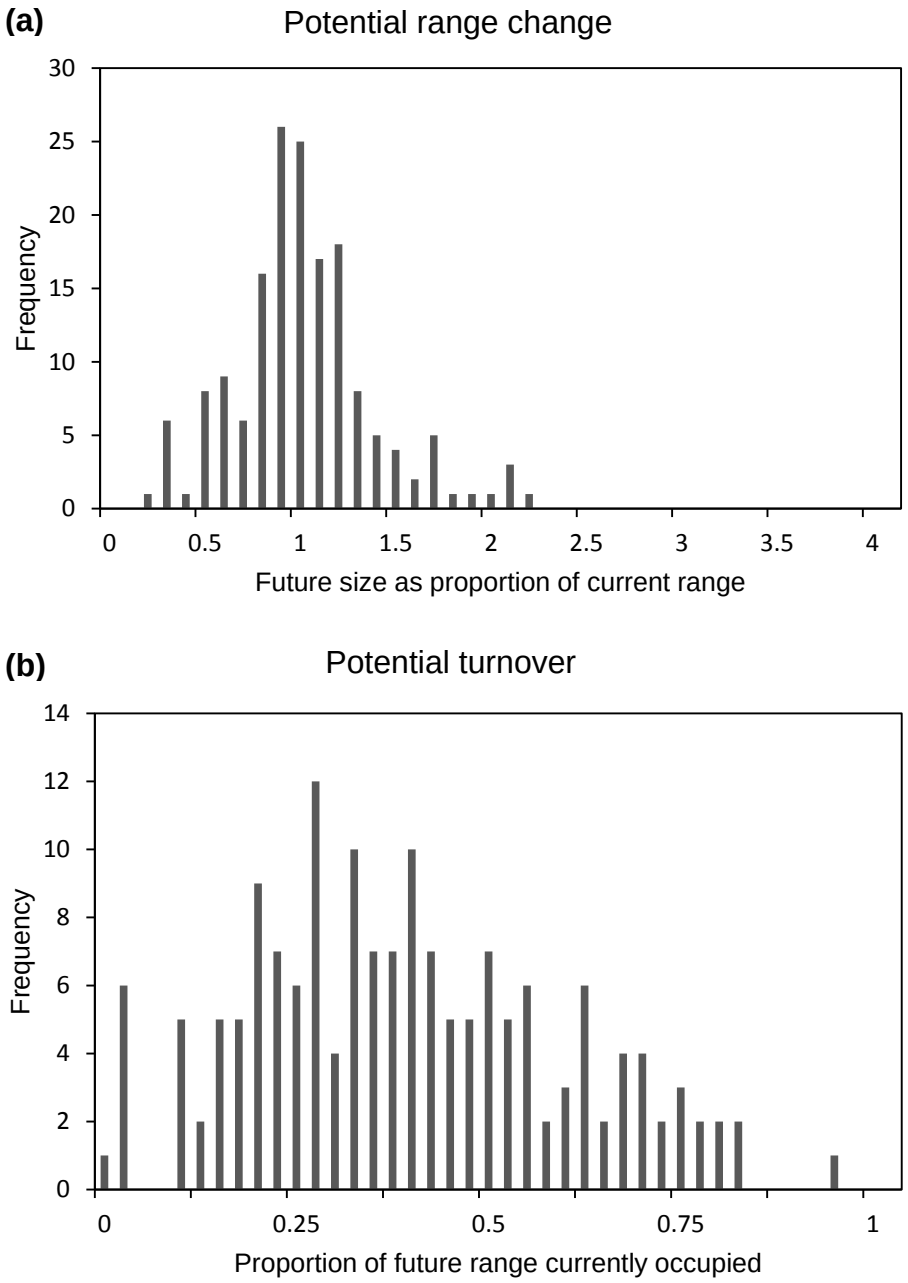

Figure 4.4 Projected A) range change and B) turnover for the 'potential' ranges of 164 species endemic to the southwestern United States. The 'potential' range encompasses all climatically suitable regions in the southwestern United States, regardless of whether it is currently occupied by the species. Additionally, I assume unlimited future migration. Range change values are obtained by dividing the number of pixels projected to be occupied in the future by those in the present. Turnover is the proportion of the future range that is currently occupied.

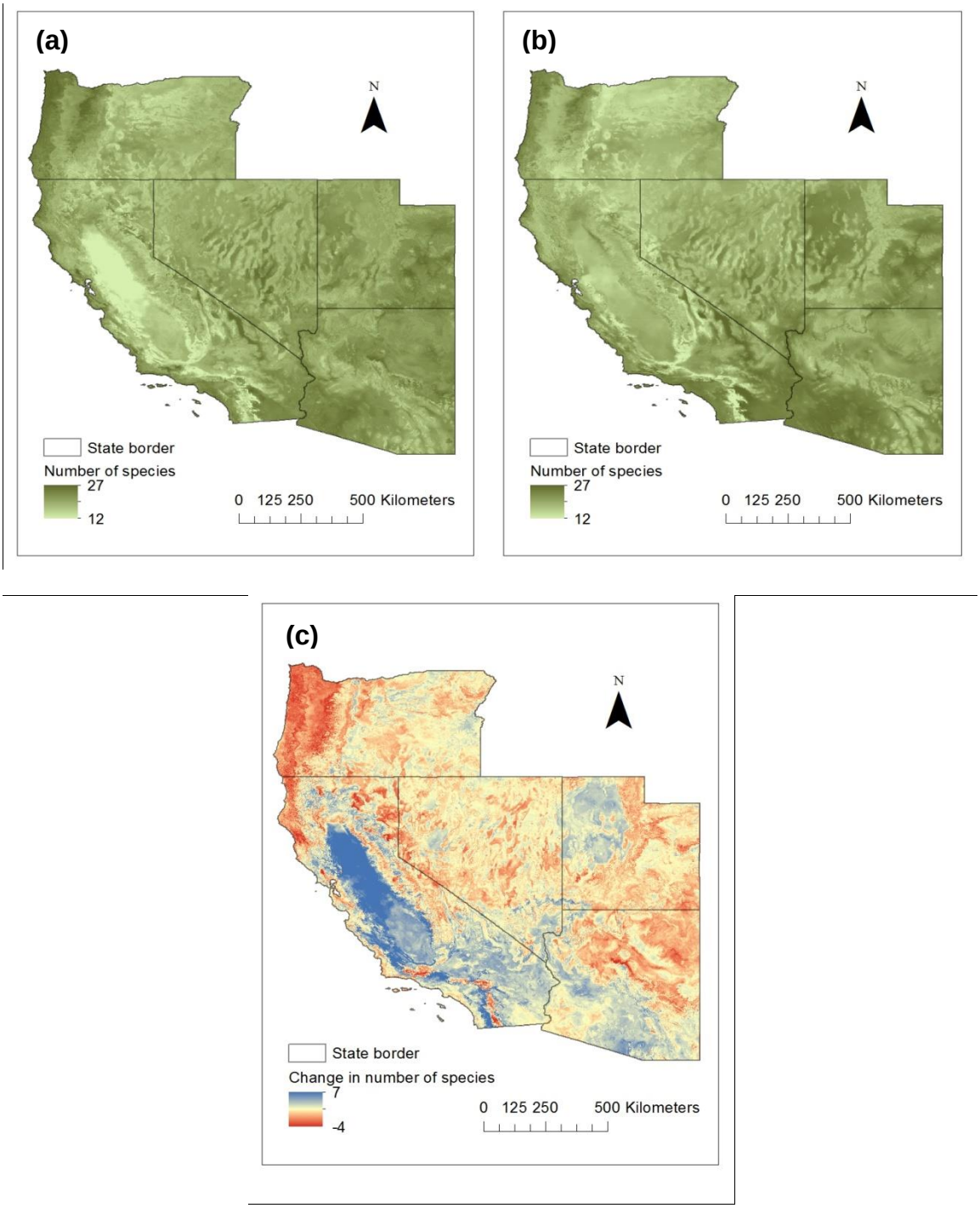

Figure 4.5 Estimates for the 'potential' ranges of A) current, B) future, and C) changes in 164 species endemic to the southwest United States. The 'potential' range encompasses all climatically suitable regions in the southwestern United States, regardless of whether it is occupied by the species. Additionally, I assume unlimited future migration.

Appendix

Mountain range	Transect number	Latitude–Longitude (degrees)	Elevation (m)
Black	1	N35.72994 W82.29137	1945
		N35.64817 W82.35632	732
	2	N35.76488 W82.26511	2036
		N35.75066 W82.21410	914
	3	N35.79946 W82.25533	1884
		N35.79818 W82.20597	823
	4	N35.73655 W82.19293	1250
		N35.73904 W82.15293	610
	5	N35.74076 W82.19190	1524
		N35.76848 W82.20597	823
Balsam	6	N35.36525 W82.98334	1554
		N35.37040 W82.93845	945
	7	N35.30319 W82.92764	1859
		N35.37389 W82.93769	945
	8	N35.30396 W82.90927	1737
		N35.37411 W82.93617	945
	16	N35.29178 W82.91759	1692
		N35.25843 W82.90906	1036
	17	N35.30560 W82.89974	1615
		N35.16955 W82.84430	716
Great Smoky	9	N35.59854 W83.25748	1341
		N35.59715 W83.26600	988
	10	N35.61383 W83.25135	1158
		N35.59892 W83.26591	988
	11	N35.71111 W83.30642	1295
		N35.70620 W83.32687	899
	12	N35.61000 W83.44814	1554
		N35.66729 W83.52262	518
Nantahala	13	N35.15623 W83.57954	1250
		N35.16323 W83.51643	701
	14	N35.24180 W83.53580	1219
		N35.26756 W83.51280	648

	15	N35.02965 W83.49442	1250
		N35.26013 W83.65738	689
Jocassee Gorges	18	N35.03455 W83.01549	671
		N35.00877 W82.99261	351

Table A.1 Transects in the southern Appalachian Mountains surveyed for plethodontid salamanders by Nelson Hairston in 1940, 1947, and 1949 and resurveyed in 2011 are listed below. For each transect the mountain range, elevation, and coordinates of the highest and lowest points are provided. The transect numbers follow Hairston (1951), except Transect 4, which is Sugar Cove.

Red score	White score	Assigned species
0	0	PLSH
0	1	PLTE
0	2	PLTE*
0	3	PLTE*
1	0	PLSH
1	1	PLSH
1	2	PLTE*
1	3	PLTE*
2	0	PLSH*
2	1	PLSH*
2	2	PLSH*
2	3	HYBRID
3	0	PLSH*
3	1	PLSH*
3	2	PLSH*
3	3	PLSH

Table A.2 Salamander identification in the Nantahala Mountains. Individual plethodontid salamanders in the Nantahala Mountains were given a score (zero to three) for red on the legs and white spots on the body. Using these scores, individuals were classified as either *Plethodon shermani* (PLSH), *Plethodon teyahalee* (PLTE), or an unidentifiable hybrid (HYBRID). Elevational range limits were delineated based on individuals marked with a *.

Mountain	Transect	PLJO	DEOR	PLGL	PLYO	Other species	Total	Notes
Black	1	10	2	0	0	26	38	UA PLYO, UA PLCY
		5	1	2	2	19	29	UP PLYO, UP PLCY
		11	4	1	0	24	40	
		18	0	1	1	4	24	
		19	1	6	8	32	66	LP DEOR
		27	0	6	4	3	40	LA DEOR
		1	0	2	0	3	6	LP PLMO
		0	0	6	2	9	17	LA PLMO
		0	0	6	1	8	15	LP PLYO
		0	0	3	0	2	5	LA PLYO
		0	0	3	0	2	5	LP PLCY
		0	0	0	0	0	0	LA PLCY
		0	0	0	0	3	3	
Black	2	2	2	0	0	11	15	
		5	1	0	0	15	21	UA PLCY
		24	0	1	0	15	40	UP PLCY
		21	4	0	0	26	51	UA PLYO
		18	1	1	1	6	27	UP PLYO
		3	0	0	1	5	9	LP PLYO
		5	0	1	0	3	9	LA PLYO
		11	1	0	0	3	15	LP DEOR
		3	0	0	0	6	9	LA DEOR
		1	0	1	0	0	2	LP PLMO
		0	0	2	0	6	8	LA PLMO
Black	3	1	21	0	0	11	33	
		16	9	0	0	12	37	UA PLCY
		9	1	1	0	6	17	UA PLYO, UP PLCY
		5	0	0	1	1	7	UP PLYO
		2	1	1	0	0	4	
		7	2	0	1	5	15	
		8	5	0	1	10	24	
		2	2	0	3	9	16	LP DEOR
		0	0	0	0	3	3	LA DEOR
		5	0	7	1	9	22	
		3	0	5	0	7	15	LP PLMO
		0	0	1	0	3	4	LA PLMO
		0	0	1	1	0	2	
Black	4	0	0	2	1	1	4	LP PLYO

		0	0	1	0	1	2	LA PLYO
		0	0	2	0	0	2	LP PLCY
		0	0	0	0	0	0	LA PLCY
		0	0	0	0	5	5	
Black	5	3	1	0	0	0	4	UA PLCY
		0	0	1	0	0	1	UP PLCY
		2	5	0	0	17	24	UA PLYO
		4	1	1	1	18	25	UP PLYO
		15	0	0	0	5	20	
		8	17	2	0	33	60	
		8	2	0	2	7	19	
		7	4	0	4	14	29	LP PLYO, LP DEOR
		0	0	3	0	0	3	LA PLYO, LA DEOR
		1	0	1	0	5	7	LP PLMO
		0	0	4	0	1	5	LA PLMO
Balsam	6	9		0		0	9	
		13		0		30	43	
		8		0		2	10	UA PLTE
		9		1		3	13	UP PLTE
		2		1		5	8	LP PLME
		0		2		3	5	LA PLME
Balsam	7	10		0		15	25	
		12		0		4	16	UA PLTE
		5		2		5	12	UP PLTE
		2		0		6	8	
		0		0		1	1	
		3		0		4	7	LP PLME
		0		4		1	5	LA PLME
Balsam	8	12		0		8	20	UA PLTE
		7		1		6	14	UP PLTE
		1		2		3	6	LP PLME
		0		1		5	6	LA PLME
Smoky	9	63		0		2	65	
		9		0		8	17	UA PLTE
		8		1		7	16	UP PLTE
		1		2		0	3	LP PLJO
		0		2		0	2	LA PLJO
Smoky	10	3		0		3	6	
		9		0		2	11	UA PLTE

		2	1	3	6	UP PLTE, LP PLJO
		0	2	2	4	LA PLJO
Smoky	11	2	0	3	5	
		3	0	3	6	LP PLJO, UA PLTE
		0	3	3	6	LA PLJO, UP PLTE
		0	1	3	4	
Smoky	12	22	0	4	26	
		11	0	2	13	
		2	0	1	3	UA PLTE
		0	1	0	1	UP PLTE
		0	2	0	2	
		3	1	1	5	LP PLJO
		0	1	1	2	LA PLJO, LP PLTE
		0	0	1	1	LA PLTE
		0	0	0	0	
		0	0	0	0	
Nantahala	13	3	0	5	8	
		8	0	9	17	
		2	0	9	11	UA PLTE
		0	1	0	1	UP PLTE
		1	2	6	9	LP PLSH
		0	1	2	3	LA PLSH
		0	1	3	4	
		0	0	1	1	
		0	3	1	4	
Nantahala	14	19	0	31	50	
		26	0	20	46	UA PLSH
		3	1	2	6	UP PLTE
		14	1	3	18	
		6	1	21	28	
		2	0	10	12	
		1	1	8	10	
		1	5	2	8	LP PLSH
		0	2	2	4	LA PLSH
		0	1	3	4	LP PLTE
		0	0	1	1	LA PLTE
Nantahala	15	6	0	17	23	
		4	0	0	4	UA PLTE
		4	1	18	23	UP PLTE

		2	3	5	10	LP PLSH
		0	2	6	8	LA PLSH
		0	3	1	4	
		0	3	0	3	
		0	1	0	1	
Balsam	16	1	0	0	1	
		6	0	0	6	UA PLTE
		6	1	0	7	UP PLTE
		4	4	1	9	
Balsam	17	4	0	8	12	
		7	0	6	13	UA PLTE
		8	1	3	12	UP PLTE
		17	2	18	37	
		1	2	1	4	
Blue Ridge	18	1	1	8	10	
		1	2	0	3	

Table A.3 Salamander data for all plots surveyed in the southern Appalachian Mountains. Each row represents a plot in the study. The mountain range, transect and number of salamanders in the *Plethodon jordani* (PLJO) and *P. glutinosus* (PLGL) complexes, and *Desmognathus organi* (DEOR) and *P. yonahlosee* (PLYO) are given for each plot. Additionally, the number of other species and the total number of salamanders encountered are provided. Plots are listed by elevation with the highest elevation occurring first. In the notes the code UA preceding the species code indicates the plot 30 m above the upper elevational range limit for that species. UP indicates the plot at the upper elevational range limit. Similarly, LP indicates the plot at the lower elevational range limit and LA the plot 30 m below that in elevation. Finally, the elevational ranges for each species have been highlighted.

Species	Test AUC	Standard AUC
Actaea arizonica	0.82	0.92
Agave delamateri	0.84	0.91
Allium hickmanii	0.87	0.92
Allium jepsonii	0.91	0.97
Allium tribracteatum	0.76	0.87
Ambystoma californiense	0.86	0.87
Amsinckia lunaris	0.72	0.85
Amsonia peeblesii	0.86	0.92
Anaxyrus canorus	0.84	0.90
Aneides ferreus	0.59	0.77
Arabis constancei	0.80	0.88
Arborimus pomo	0.76	0.85
Arctostaphylos hookeri ssp. montana	0.73	0.86
Arctostaphylos rainbowensis	0.77	0.89
Astragalus agnicidus	0.75	0.87
Astragalus cremnophylax var. hevronii	0.69	0.82
Astragalus lentiformis	0.82	0.90
Astragalus leucolobus	0.90	0.96
Astragalus xiphoides	0.74	0.86
Batrachoseps wrightorum	0.81	0.88
Blennosperma bakeri	0.95	0.97
Blepharizonia plumosa	0.83	0.92
Brodiaea filifolia	0.87	0.93
Calochortus clavatus	0.83	0.90
Calochortus excavatus	0.82	0.91
Calochortus obispoensis	0.83	0.93
Calochortus palmeri	0.90	0.94
Calochortus plummerae	0.70	0.84
Calochortus pulchellus	0.85	0.91
Calochortus weedii	0.79	0.88
Calochortus westonii	0.83	0.92
Calycadenia hooveri	0.81	0.87
Calycadenia villosa	0.78	0.86
Calystegia atriplicifolia	0.92	0.95
Calystegia subacaulis ssp. episcopalis	0.71	0.83
Camissonia benitensis	0.76	0.90
Campanula californica	0.93	0.95
Castilleja cinerea	0.89	0.95

Castilleja lasiorhyncha	0.73	0.88
Ceanothus purpureus	0.81	0.91
Chlorogalum grandiflorum	0.66	0.79
Chorizanthe breweri	0.86	0.93
Chorizanthe parryi	0.84	0.91
Chorizanthe rectispina	0.67	0.84
Chrysothamnus molestus	0.85	0.90
Cirsium fontinale	0.85	0.90
Cirsium loncholepis	0.93	0.97
Clarkia australis	0.83	0.93
Clarkia biloba	0.67	0.81
Clarkia borealis ssp. borealis	0.69	0.82
Clarkia mildrediae	0.71	0.84
Clarkia mosquinii	0.78	0.86
Cordylanthus tenuis	0.81	0.88
Coreopsis hamiltonii	0.73	0.91
Cryptantha crinita	0.71	0.84
Cymopterus deserticola	0.87	0.91
Cymopterus gilmanii	0.84	0.90
Cymopterus megacephalus	0.69	0.84
Delphinium hesperium ssp. cuyamacae	0.87	0.96
Delphinium hutchinsoniae	0.83	0.92
Delphinium inopinum	0.88	0.93
Dipodomys ingens	0.76	0.88
Dipodomys stephensi	0.75	0.87
Dirca occidentalis	0.65	0.83
Dodecahema leptoceras	0.80	0.89
Dudleya multicaulis	0.83	0.92
Dudleya setchellii	0.80	0.90
Epilobium howellii	0.68	0.81
Eriastrum brandegeeae	0.85	0.91
Erigeron parishii	0.75	0.88
Eriogonum hirtellum	0.72	0.82
Eriophyllum mohavense	0.79	0.89
Erythronium citrinum	0.88	0.92
Euphorbia aaron-rossii	0.90	0.96
Euphydryas editha quino	0.82	0.87
Fritillaria brandegeei	0.89	0.92
Fritillaria liliacea	0.71	0.86
Fritillaria pluriflora	0.86	0.92

Fritillaria striata	0.72	0.88
Grindelia hirsutula	0.90	0.95
Hedeoma diffusa	0.90	0.95
Helianthella castanea	0.80	0.89
Helminthoglypta hertleini	0.79	0.88
Hemizonia minthornii	0.79	0.89
Hemizonia parryi	0.92	0.94
Hemizonia pungens	0.91	0.95
Hesperarion mariae	0.64	0.82
Hesperodoria scopulorum	0.78	0.90
Hesperolinon adenophyllum	0.62	0.81
Hesperolinon congestum	0.80	0.87
Hoita strobilina	0.84	0.89
Holocarpha macradenia	0.93	0.94
Horkelia tenuiloba	0.82	0.90
Ivesia multifoliolata	0.76	0.87
Ivesia sericoleuca	0.87	0.93
Lasthenia burkei	0.84	0.92
Layia heterotricha	0.81	0.88
Lessingia micradenia	0.82	0.90
Lewisia cantelovii	0.87	0.93
Lilium maritimum	0.90	0.95
Limnanthes floccosa	0.82	0.88
Limnanthes vinculans	0.90	0.96
Lithobates onca	0.75	0.91
Lomatium stebbinsii	0.82	0.92
Lupinus citrinus	0.83	0.88
Lupinus dalesiae	0.86	0.90
Lupinus sericatus	0.70	0.86
Madia doris-nilesiae	0.64	0.76
Mahonia nevinii	0.75	0.87
Mimulus filicaulis	0.72	0.89
Mimulus mohavensis	0.79	0.91
Monadenia infumata setosa	0.73	0.87
Monardella follettii	0.86	0.94
Monardella robisonii	0.90	0.96
Oreonana purpurascens	0.79	0.93
Packera layneae	0.86	0.92
Paronychia ahartii	0.83	0.90
Pediocactus bradyi	0.87	0.94

Pediocactus paradinei	0.91	0.96
Pediocactus peeblesianus	0.83	0.93
Penstemon clutei	0.87	0.92
Penstemon filiformis	0.77	0.85
Pentachaeta lyonii	0.79	0.89
Phacelia dalesiana	0.79	0.91
Phacelia greenei	0.60	0.82
Phacelia nashiana	0.78	0.87
Phacelia novenmillensis	0.82	0.90
Phacelia stebbinsii	0.66	0.80
Plethodon elongatus	0.65	0.81
Plethodon stormi	0.72	0.81
Pogogyne abramsii	0.94	0.97
Polygala acanthoclada	0.89	0.94
Pseudobahia peirsonii	0.78	0.89
Pyrrocoma lucida	0.89	0.93
Rana muscosa	0.89	0.93
Rana sierrae	0.86	0.91
Reithrodontomys raviventris	0.81	0.89
Rhyacotriton variegatus	0.85	0.89
Rupertia hallii	0.83	0.93
Sairocarpus subcordatus	0.80	0.91
Sanicula tracyi	0.90	0.93
Scrophularia atrata	0.71	0.86
Sedum laxum	0.76	0.87
Sidalcea covillei	0.76	0.90
Silene marmorensis	0.84	0.93
Speyeria carolae	0.85	0.94
Stanfordia californica	0.91	0.96
Streptanthus albidus	0.79	0.90
Streptanthus gracilis	0.76	0.88
Stylocline citroleum	0.91	0.93
Talinum validulum	0.88	0.91
Taraxacum californicum	0.90	0.96
Taricha torosa	0.84	0.93
Thamnophis gigas	0.86	0.91
Thermopsis californica	0.83	0.94
Thermopsis robusta	0.75	0.88
Triphysaria floribunda	0.93	0.95
Triteleia hendersonii	0.77	0.85

Triteleia lemmoniae	0.79	0.88
Uma scoparia	0.81	0.92
Viola pinetorum	0.93	0.94
Viola tomentosa	0.81	0.89
Wyethia reticulata	0.83	0.91
Xerospermophilus mohavensis	0.62	0.81

Table A.4 Listed alphabetically are the 164 species used in the analysis. The area under the curve (AUC) scores for both the 'test' and standard minimum convex polygon buffered by 25 km are given for each species. Additionally, the species used for the ANOVA are in bold.

	Realized Extent						Potential Extent					
	Range size change			Turnover			Range size change			Turnover		
Species	0.05	Median	0.95	0.05	Median	0.95	0.05	Median	0.95	0.05	Median	0.95
Actaea arizonica	0.00	0.07	1.48	0.00	0.41	1.00	0.01	0.69	1.30	0.00	0.73	0.99
Agave delamateri	0.03	1.73	4.38	0.00	0.17	0.38	0.41	1.36	4.97	0.00	0.14	0.92
Allium hickmanii	0.00	0.01	11.11	0.01	0.33	1.00	0.00	0.29	3.15	0.00	0.66	1.00
Allium jepsonii	0.00	0.19	1.99	0.00	0.50	0.98	0.36	1.00	5.22	0.00	0.23	0.94
Allium tribracteatum	0.00	0.34	1.87	0.00	0.18	0.91	0.09	0.94	1.67	0.00	0.29	1.00
Ambystoma californiense	0.03	0.51	1.92	0.19	0.48	0.82	0.13	0.91	1.82	0.13	0.55	0.94
Amsinckia lunaris	0.00	0.34	1.81	0.00	0.57	1.00	0.00	0.86	2.16	0.00	0.55	0.95
Amsonia peeblesii	0.41	2.93	9.81	0.00	0.15	0.29	0.66	1.68	6.29	0.00	0.37	0.71
Anaxyrus canorus	0.00	0.33	1.72	0.00	0.49	1.00	0.05	0.74	2.33	0.00	0.74	1.00
Aneides ferreus	0.00	0.47	1.93	0.00	0.39	0.96	0.02	0.81	2.24	0.00	0.37	0.92
Arabis constancei	0.02	1.82	7.38	0.00	0.11	0.42	0.29	1.14	2.11	0.00	0.45	0.83
Arborimus pomo	0.00	0.74	3.60	0.00	0.33	1.00	0.20	0.99	4.10	0.00	0.53	1.00
Arctostaphylos hookeri ssp. montana	0.06	0.68	1.87	0.01	0.79	1.00	0.13	0.77	1.60	0.00	0.64	0.98
Arctostaphylos rainbowensis	0.00	0.47	4.23	0.00	0.07	0.78	0.00	0.91	3.50	0.00	0.08	0.89
Astragalus agnicidus	0.00	0.02	1.36	0.00	0.29	0.95	0.00	0.47	1.78	0.00	0.16	0.96
Astragalus cremnophylax var. hevronii	0.00	0.26	1.89	0.00	0.42	1.00	0.00	0.84	1.74	0.00	0.40	0.89
Astragalus lentiformis	0.00	0.00	3.60	0.00	0.28	0.99	0.01	0.59	1.62	0.00	0.43	0.99
Astragalus leucolobus	0.00	0.06	1.65	0.00	0.62	1.00	0.00	0.77	7.30	0.00	0.68	0.99
Astragalus xiphoides	0.00	0.01	2.28	0.00	0.12	0.68	0.00	0.72	2.33	0.00	0.17	0.69
Batrachoseps wrightorum	0.01	0.35	1.08	0.00	0.29	0.70	0.04	0.43	1.55	0.00	0.40	0.87
Blennosperma bakeri	0.00	0.00	6.28	0.00	0.35	1.00	0.00	0.73	2.19	0.00	0.43	0.99
Blepharizonia plumosa	0.00	0.49	3.78	0.00	0.19	0.73	0.28	1.16	3.64	0.00	0.27	0.94
Brodiaea filifolia	0.02	1.03	3.28	0.04	0.42	0.98	0.22	1.04	2.59	0.02	0.61	0.99

Calochortus clavatus	0.04	0.71	1.91	0.00	0.29	0.63	0.24	0.91	1.97	0.00	0.40	0.92
Calochortus excavatus	0.00	0.00	0.74	0.00	0.87	1.00	0.00	0.79	2.00	0.00	0.70	1.00
Calochortus obispoensis	0.00	0.10	0.90	0.21	0.99	1.00	0.00	0.28	1.05	0.00	0.71	1.00
Calochortus palmeri	0.00	0.19	1.88	0.00	0.20	0.69	0.00	1.06	2.68	0.00	0.26	0.96
Calochortus plummerae	0.00	0.41	2.36	0.00	0.24	0.71	0.23	0.95	1.75	0.00	0.24	0.95
Calochortus pulchellus	0.16	1.18	2.13	0.00	0.45	0.83	0.47	1.24	2.86	0.00	0.38	0.81
Calochortus weedii	0.00	0.01	3.43	0.00	0.05	0.99	0.22	0.94	2.97	0.00	0.21	1.00
Calochortus westonii	0.00	0.21	1.53	0.00	0.27	0.77	0.00	0.87	1.73	0.00	0.27	0.89
Calycadenia hooveri	0.00	1.93	6.47	0.00	0.20	0.92	0.02	1.50	7.54	0.00	0.32	0.92
Calycadenia villosa	0.00	0.29	1.14	0.00	0.64	0.92	0.10	0.74	1.87	0.00	0.58	0.95
Calystegia atriplicifolia	0.02	1.18	2.40	0.00	0.45	0.83	0.74	1.66	3.73	0.00	0.38	0.76
Calystegia subacaulis ssp. episcopalis	0.00	0.47	3.92	0.00	0.27	0.89	0.00	1.04	2.85	0.00	0.60	0.95
Camissonia benitensis	0.00	0.48	13.60	0.00	0.18	1.00	0.02	0.57	6.23	0.00	0.17	0.96
Campanula californica	0.00	0.21	2.08	0.00	0.42	0.87	0.01	1.15	3.96	0.00	0.19	0.85
Castilleja cinerea	0.00	0.39	2.64	0.00	0.45	0.98	0.01	0.86	5.20	0.00	0.41	0.99
Castilleja lasiorhyncha	0.00	0.88	3.13	0.03	0.44	0.82	0.46	0.98	1.57	0.05	0.67	0.94
Ceanothus purpureus	0.00	0.29	2.70	0.00	0.04	0.67	0.22	0.96	3.22	0.00	0.13	0.97
Chlorogalum grandiflorum	0.00	0.90	7.17	0.00	0.20	0.93	0.67	1.23	7.47	0.00	0.21	0.91
Chorizanthe breweri	0.00	0.33	1.99	0.00	0.00	0.44	0.00	1.08	2.23	0.00	0.00	0.70
Chorizanthe parryi	0.00	0.04	0.88	0.00	0.03	0.68	0.00	0.21	1.74	0.00	0.02	0.61
Chorizanthe rectispina	0.10	1.88	3.95	0.00	0.25	0.49	0.91	2.07	8.51	0.00	0.19	0.82
Chrysothamnus molestus	0.00	0.32	3.46	0.00	0.56	1.00	0.00	0.64	2.92	0.00	0.37	0.99
Cirsium fontinale	0.00	0.40	4.07	0.00	0.20	0.85	0.00	0.97	2.18	0.00	0.35	0.99
Cirsium loncholepis	0.00	0.00	2.74	0.00	0.19	0.61	0.00	0.16	2.79	0.00	0.00	0.94
Clarkia australis	0.00	0.21	3.33	0.00	0.08	0.91	0.00	0.80	1.69	0.00	0.22	0.99
Clarkia biloba	0.24	2.02	56.62	0.01	0.19	0.48	0.50	1.05	1.47	0.06	0.82	0.97
Clarkia borealis ssp. borealis	0.00	0.89	2.88	0.00	0.22	0.87	0.28	1.10	3.95	0.00	0.18	0.99

Clarkia mildrediae	0.00	1.06	2.68	0.00	0.18	0.62	0.22	1.21	4.39	0.00	0.17	0.71
Clarkia mosquinii	0.03	2.28	16.43	0.00	0.24	0.42	0.45	1.95	5.79	0.01	0.43	0.93
Cordylanthus tenuis	0.00	0.00	1.85	0.00	0.33	0.99	0.10	0.85	1.68	0.00	0.58	0.99
Coreopsis hamiltonii	0.00	0.29	1.49	0.00	0.29	0.98	0.11	0.89	1.53	0.00	0.21	0.95
Cryptantha crinita	0.00	0.67	2.81	0.00	0.42	0.95	0.36	1.01	1.85	0.00	0.65	0.99
Cymopterus deserticola	0.00	0.03	4.80	0.00	0.19	0.61	0.00	0.96	1.91	0.00	0.37	0.90
Cymopterus gilmanii	0.00	0.50	1.68	0.00	0.43	0.83	0.13	0.85	3.67	0.00	0.51	0.91
Cymopterus megacephalus	0.00	0.52	2.85	0.00	0.36	1.00	0.00	1.39	3.51	0.00	0.27	0.91
Delphinium hesperium ssp. cuyamacae	0.00	0.01	3.64	0.00	0.49	1.00	0.12	0.83	2.08	0.00	0.61	0.99
Delphinium hutchinsoniae	0.00	0.43	2.41	0.00	0.69	1.00	0.00	0.81	1.91	0.00	0.58	0.95
Delphinium inopinum	0.00	0.50	1.20	0.00	0.38	0.80	0.00	0.59	1.86	0.00	0.31	0.95
Dipodomys ingens	0.00	1.81	5.61	0.00	0.26	0.72	0.15	1.10	2.93	0.00	0.47	0.91
Dipodomys stephensi	0.00	0.85	3.24	0.00	0.36	0.96	0.00	1.03	4.78	0.00	0.40	0.97
Dirca occidentalis	0.00	0.57	2.81	0.00	0.42	1.00	0.12	1.18	3.41	0.00	0.34	0.99
Dodecahema leptoceras	0.00	1.47	18.07	0.00	0.20	0.65	0.04	1.76	4.99	0.00	0.25	0.85
Dudleya multicaulis	0.00	2.25	4.30	0.00	0.26	0.47	0.18	2.14	5.66	0.00	0.22	0.74
Dudleya setchellii	0.00	0.25	2.86	0.00	0.08	0.81	0.00	0.88	2.21	0.00	0.26	0.97
Epilobium howellii	0.00	0.42	2.52	0.00	0.07	0.69	0.01	0.42	1.25	0.00	0.18	0.92
Eriastrum brandegeeae	0.00	0.52	1.58	0.00	0.29	0.65	0.58	1.24	2.94	0.00	0.32	0.96
Erigeron parishii	0.00	1.04	3.47	0.00	0.20	0.62	0.31	1.35	4.15	0.00	0.26	0.87
Eriogonum hirtellum	0.00	0.35	1.88	0.00	0.57	1.00	0.01	0.58	1.85	0.00	0.50	1.00
Eriophyllum mohavense	0.00	0.13	3.11	0.00	0.14	0.94	0.00	1.11	8.77	0.00	0.08	0.89
Erythronium citrinum	0.00	0.40	1.31	0.00	0.21	0.95	0.09	0.72	1.35	0.00	0.20	0.96
Euphorbia aaron-rossii	0.48	3.34	8.29	0.01	0.18	0.46	0.90	2.05	20.53	0.00	0.26	0.62
Euphydryas editha quino	0.08	0.74	2.06	0.00	0.31	0.80	0.40	1.29	3.66	0.00	0.31	0.94
Fritillaria brandegeei	0.00	0.27	1.96	0.07	0.39	0.89	0.05	0.78	1.61	0.00	0.52	0.98
Fritillaria liliacea	0.00	0.41	3.18	0.00	0.38	1.00	0.02	0.68	2.89	0.00	0.43	0.97

Fritillaria pluriflora	0.00	0.17	2.05	0.00	0.20	0.74	0.19	0.98	2.22	0.00	0.31	0.93
Fritillaria striata	0.00	0.58	3.65	0.00	0.26	0.93	0.00	0.95	2.89	0.00	0.30	0.96
Grindelia hirsutula	0.00	0.04	2.92	0.02	0.79	1.00	0.38	0.83	1.49	0.00	0.93	1.00
Hedeoma diffusa	0.00	0.65	4.48	0.00	0.27	0.87	0.03	1.16	3.06	0.00	0.41	0.94
Helianthella castanea	0.00	0.27	2.77	0.00	0.27	0.80	0.02	0.86	2.30	0.00	0.31	0.94
Helminthoglypta hertleini	0.00	2.44	13.07	0.00	0.18	0.47	0.01	1.37	6.31	0.00	0.35	0.88
Hemizonia minthornii	0.00	0.90	5.42	0.01	0.25	0.68	0.01	0.91	3.33	0.00	0.47	0.91
Hemizonia parryi	0.12	1.53	2.33	0.00	0.45	0.65	0.15	1.14	1.91	0.00	0.56	0.75
Hemizonia pungens	0.00	0.66	3.94	0.00	0.20	1.00	0.03	0.91	4.30	0.00	0.40	0.99
Hesperarion mariae	0.00	0.89	3.87	0.00	0.24	0.82	0.40	1.62	6.46	0.00	0.20	0.83
Hesperodoria scopulorum	0.09	0.92	4.28	0.00	0.32	0.91	0.14	0.93	3.12	0.00	0.49	0.91
Hesperolinon adenophyllum	0.00	0.90	5.23	0.00	0.20	0.80	0.22	1.23	3.69	0.00	0.41	0.92
Hesperolinon congestum	0.00	0.18	1.37	0.00	0.36	0.95	0.12	0.75	1.55	0.00	0.50	0.85
Hoita strobilina	0.00	0.08	2.42	0.00	0.22	0.94	0.00	0.24	2.09	0.00	0.13	0.96
Holocarpha macradenia	0.00	1.12	30.41	0.00	0.26	0.92	0.04	1.14	5.30	0.00	0.32	0.93
Horkelia tenuiloba	0.00	0.81	4.91	0.00	0.44	1.00	0.50	0.90	4.66	0.01	0.78	1.00
Ivesia multifoliolata	0.00	0.11	1.50	0.00	0.20	0.78	0.00	0.73	2.18	0.00	0.20	0.78
Ivesia sericoleuca	0.00	0.01	1.13	0.00	0.68	1.00	0.01	0.25	1.23	0.00	0.40	0.98
Lasthenia burkei	0.00	0.30	4.62	0.00	0.34	1.00	0.00	0.81	2.42	0.00	0.38	0.98
Layia heterotricha	0.00	0.34	2.29	0.00	0.63	1.00	0.11	0.92	4.37	0.00	0.44	1.00
Lessingia micradenia	0.00	0.75	3.21	0.00	0.07	0.46	0.06	0.84	2.27	0.00	0.08	0.81
Lewisia cantelovii	0.00	0.38	3.18	0.00	0.11	0.82	0.00	0.81	4.36	0.00	0.10	0.97
Lilium maritimum	0.00	0.55	2.00	0.00	0.31	0.95	0.35	1.07	2.60	0.00	0.34	0.97
Limnanthes floccosa	0.00	0.00	0.61	0.00	0.97	1.00	0.00	0.37	1.55	0.00	0.55	1.00
Limnanthes vinculans	0.01	2.38	8.20	0.00	0.21	0.59	0.11	1.86	12.11	0.00	0.14	0.80
Lithobates onca	0.00	0.05	7.54	0.00	0.14	1.00	0.00	0.83	2.36	0.00	0.49	0.98
Lomatium stebbinsii	0.00	0.23	1.55	0.00	0.09	0.80	0.35	1.11	2.52	0.01	0.27	0.97
Lupinus citrinus	0.02	1.15	3.73	0.02	0.38	0.89	0.66	1.11	2.57	0.03	0.60	0.95

Lupinus dalesiae	0.03	1.47	4.40	0.00	0.08	0.35	0.36	1.00	1.93	0.00	0.35	0.85
Lupinus sericatus	0.00	0.71	3.23	0.00	0.48	1.00	0.08	0.90	8.39	0.00	0.62	1.00
Madia doris-nilesiae	0.00	0.23	5.96	0.00	0.09	0.72	0.05	1.07	3.07	0.00	0.12	0.87
Mahonia nevinii	0.19	2.83	30.37	0.00	0.18	0.56	0.55	2.05	22.15	0.00	0.28	0.75
Mimulus filicaulis	0.00	0.13	1.63	0.00	0.31	0.96	0.16	0.97	1.91	0.00	0.37	0.96
Mimulus mohavensis	0.00	1.23	10.36	0.00	0.10	0.36	0.41	1.15	4.89	0.00	0.48	0.96
Monadenia infumata setosa	0.00	3.46	6.91	0.00	0.15	0.35	0.22	1.28	3.00	0.00	0.46	0.87
Monardella follettii	0.00	0.39	5.54	0.00	0.01	0.71	0.00	1.03	5.75	0.00	0.02	0.83
Monardella robisonii	0.00	0.09	6.02	0.00	0.20	0.86	0.05	0.83	1.91	0.00	0.66	1.00
Oreonana purpurascens	0.00	0.54	1.38	0.00	0.28	0.76	0.03	0.42	1.31	0.00	0.46	0.92
Packera layneae	0.00	0.06	3.97	0.00	0.00	0.44	0.02	0.86	2.39	0.00	0.01	0.93
Paronychia ahartii	0.00	0.05	2.26	0.00	0.19	0.84	0.00	0.54	1.88	0.00	0.12	0.88
Pediocactus bradyi	0.00	2.25	7.62	0.00	0.17	0.76	0.25	1.34	5.14	0.00	0.67	0.90
Pediocactus paradinei	0.00	0.62	4.77	0.00	0.05	0.50	0.08	0.75	1.63	0.00	0.31	0.94
Pediocactus peeblesianus	0.00	0.47	2.09	0.00	0.28	1.00	0.43	1.06	2.61	0.00	0.52	0.94
Penstemon clutei	0.00	0.74	4.34	0.00	0.22	0.75	0.09	1.10	3.57	0.00	0.54	0.99
Penstemon filiformis	0.00	0.79	4.15	0.00	0.10	0.57	0.52	1.01	1.71	0.00	0.20	0.89
Pentachaeta lyonii	0.00	0.73	2.56	0.00	0.12	0.47	0.22	1.42	4.58	0.00	0.08	0.78
Phacelia dalesiana	0.00	0.11	2.37	0.00	0.45	1.00	0.11	0.79	2.50	0.00	0.36	0.98
Phacelia greenei	0.00	0.08	1.95	0.00	0.08	0.99	0.06	0.92	3.07	0.00	0.26	1.00
Phacelia nashiana	0.08	1.59	4.17	0.00	0.27	0.74	0.25	1.05	4.74	0.00	0.28	0.98
Phacelia novenmillensis	0.00	0.39	1.64	0.00	0.32	0.99	0.03	0.62	2.10	0.00	0.24	0.96
Phacelia stebbinsii	0.00	1.00	2.18	0.00	0.32	0.86	0.07	1.08	2.51	0.00	0.29	0.90
Plethodon elongatus	0.00	0.54	1.54	0.00	0.65	0.99	0.07	0.82	2.10	0.00	0.48	0.98
Plethodon stormi	0.04	0.41	3.62	0.00	0.20	0.48	0.39	1.11	1.96	0.00	0.26	0.82
Pogogyne abramsii	0.00	0.00	1.45	0.00	0.05	0.35	0.00	0.77	1.30	0.00	0.19	0.99
Polygala acanthoclada	0.29	4.02	33.25	0.00	0.18	0.46	0.51	1.68	5.01	0.00	0.48	0.77
Pseudobahia peirsonii	0.00	0.19	3.98	0.00	0.00	0.36	0.11	1.63	7.61	0.00	0.00	0.89

Pyrrocoma lucida	0.00	0.15	3.76	0.00	0.06	0.64	0.08	0.57	1.55	0.00	0.17	0.98
Rana muscosa	0.08	0.99	2.13	0.00	0.59	0.98	0.66	1.06	2.36	0.03	0.73	0.97
Rana sierrae	0.03	0.32	1.41	0.07	0.72	1.00	0.10	0.45	1.80	0.17	0.77	0.99
Reithrodontomys raviventris	0.00	0.20	2.99	0.00	0.50	1.00	0.02	0.58	1.76	0.00	0.60	0.99
Rhyacotriton variegatus	0.04	1.15	2.44	0.01	0.41	0.83	0.07	1.11	2.75	0.01	0.40	0.84
Rupertia hallii	0.00	0.51	1.39	0.00	0.10	0.55	0.01	0.71	1.46	0.00	0.23	0.95
Sairocarpus subcordatus	0.00	0.21	2.65	0.00	0.08	0.75	0.36	1.10	5.62	0.00	0.19	0.87
Sanicula tracyi	0.00	0.29	1.39	0.00	0.34	0.83	0.01	0.65	1.52	0.00	0.39	0.86
Scrophularia atrata	0.00	0.12	2.94	0.00	0.36	1.00	0.00	0.69	3.89	0.00	0.27	1.00
Sedum laxum	0.01	0.25	0.96	0.00	0.49	0.82	0.17	0.59	1.59	0.00	0.33	0.96
Sidalcea covillei	0.12	1.26	4.47	0.00	0.41	0.83	0.36	1.50	3.27	0.01	0.37	0.86
Silene marmorensis	0.00	1.94	7.51	0.00	0.26	0.59	0.55	1.54	3.71	0.00	0.38	0.80
Speyeria carolae	0.00	0.50	4.65	0.07	0.69	1.00	0.38	0.79	1.92	0.36	0.79	0.94
Stanfordia californica	0.00	0.64	3.07	0.00	0.34	0.91	0.05	0.92	2.19	0.00	0.39	0.98
Streptanthus albidus	0.00	0.09	3.19	0.00	0.12	0.78	0.00	0.86	2.09	0.00	0.19	0.97
Streptanthus gracilis	0.00	0.40	6.67	0.00	0.03	0.30	0.13	1.58	5.33	0.00	0.25	0.95
Stylocline citroleum	0.00	0.62	1.85	0.00	0.20	0.63	0.00	0.49	1.36	0.00	0.33	0.91
Talinum validulum	0.00	0.06	1.14	0.00	0.68	1.00	0.00	0.25	1.61	0.00	0.72	0.98
Taraxacum californicum	0.08	0.91	3.22	0.01	0.51	0.89	0.46	0.95	3.55	0.02	0.75	0.96
Taricha torosa	0.00	0.28	2.39	0.00	0.29	0.90	0.27	0.91	2.22	0.00	0.56	0.95
Thamnophis gigas	0.00	0.00	2.12	0.00	0.86	1.00	0.18	0.46	2.20	0.01	0.82	1.00
Thermopsis californica	0.00	1.16	6.54	0.00	0.20	0.66	0.31	1.11	4.91	0.00	0.49	0.99
Thermopsis robusta	0.03	1.15	3.37	0.00	0.02	0.32	0.38	1.22	4.77	0.00	0.02	0.71
Triphysaria floribunda	0.00	0.01	6.30	0.05	0.67	1.00	0.00	0.47	2.27	0.00	0.69	1.00
Triteleia hendersonii	0.09	1.58	5.17	0.00	0.26	0.86	0.25	1.10	3.55	0.01	0.53	0.91
Triteleia lemmoniae	0.00	0.39	3.83	0.00	0.28	1.00	0.39	0.96	3.58	0.00	0.70	0.98
Uma scoparia	0.00	0.70	5.42	0.00	0.14	0.66	0.01	1.49	9.34	0.00	0.15	0.65
Viola pinetorum	0.00	0.86	5.42	0.00	0.37	0.73	0.04	0.90	3.75	0.00	0.40	0.90

Viola tomentosa	0.00	0.66	1.27	0.00	0.19	0.51	0.02	0.87	2.23	0.00	0.32	0.80
Wyethia reticulata	0.00	0.00	4.24	0.00	0.19	0.51	0.00	0.56	2.76	0.00	0.23	0.90
Xerospermophilus mohavensis	0.00	0.44	1.56	0.00	0.54	0.93	0.05	0.94	1.54	0.00	0.52	0.96

Table A.5 The medians and 90% confidence intervals are given for range size change and turnover metrics for both the 'realized' and 'potential' extents. The 164 species are listed alphabetically.

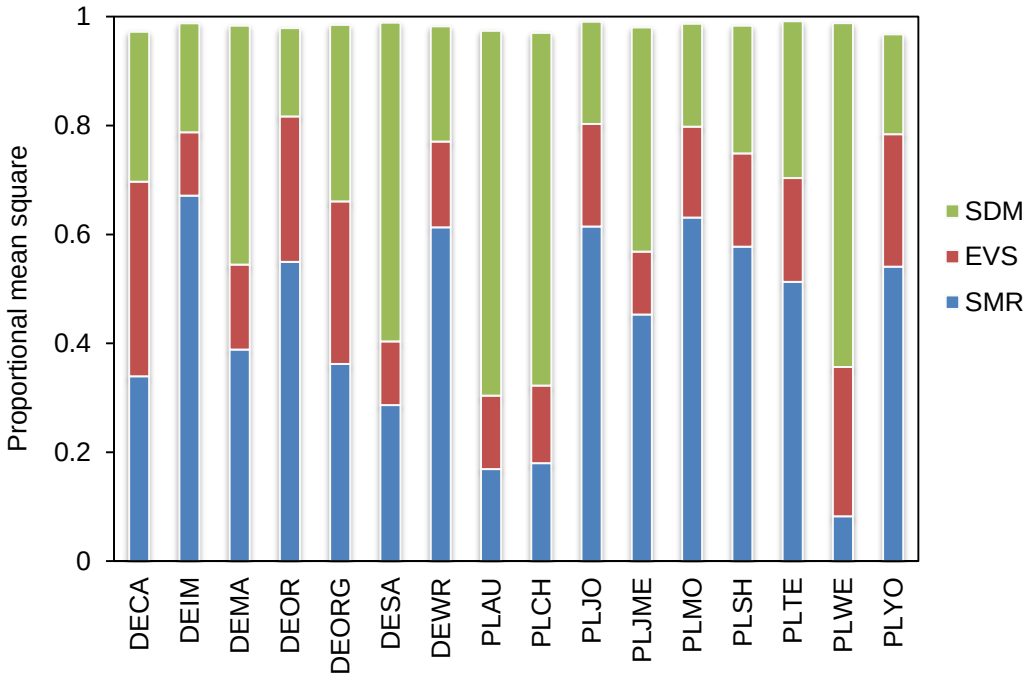

Figure A.1 The average proportional mean square for spatial modeling region (SMR), environmental variable subset (EVS), and statistical modeling method (SDM) provided by species for current projections (1970-2000). 'Training' and pseudo-absence replicates are not displayed, however account for the remaining proportional mean square. For species codes see Table 3.1.

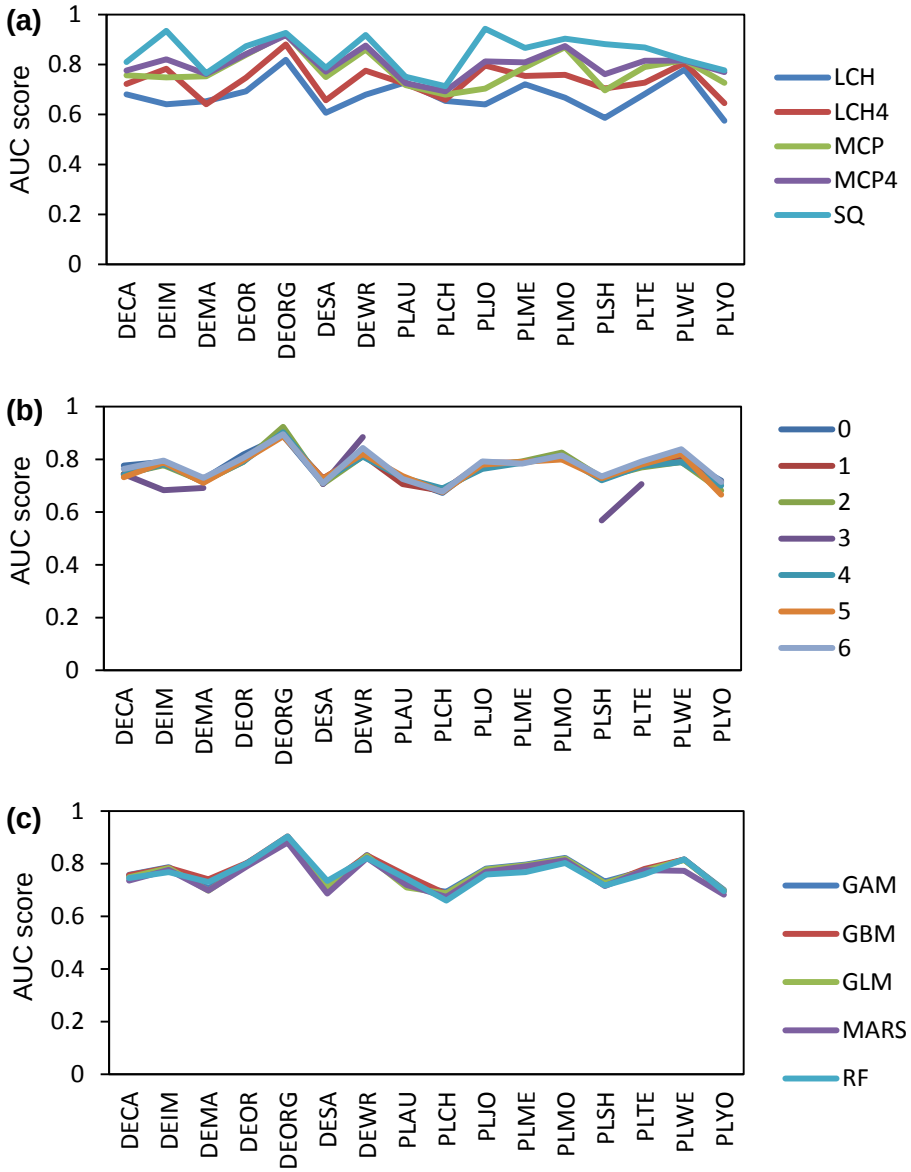

Figure A.2 The average area under the curve (AUC) scores for each level in (a) spatial modeling region, (b) environmental variable subset, and (c) statistical modeling method are provided. AUC values were calculated using the withheld 20% 'test' data. For species codes see Table 3.1. Models were built on the following backgrounds: local convex hull (LCH), LCH buffered by 4 km (LCH4), minimum convex polygon (MCP), MCP buffered by 4 km (MCP4), and MCP4 excluding 2km around presence points (SQ). Environmental variable subsets 0-3 were created by an automated procedure and subsets 4-6 were selected from the literature. For the statistical modeling method the algorithms were generalized additive models (GAM), generalized boosted models (GBM), generalized linear models (GLM), multivariate adaptive regression splines (MARS), and random forest (RF).

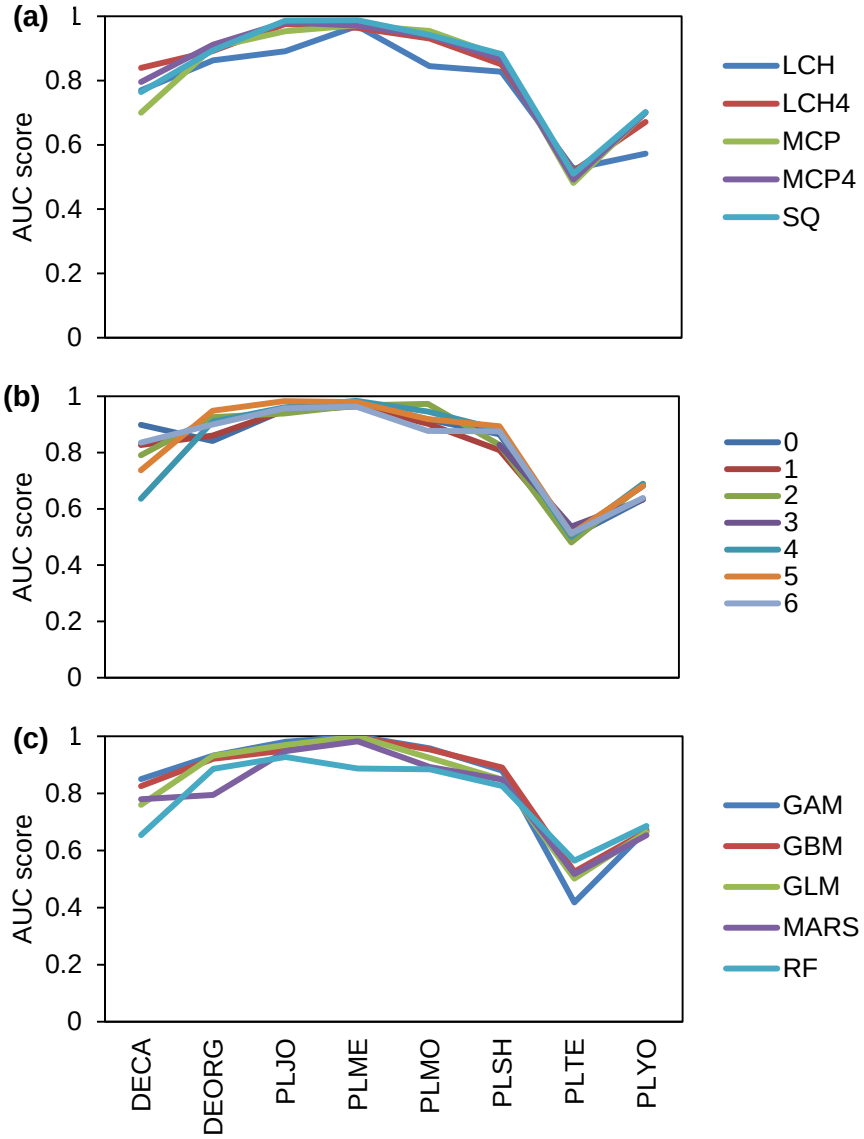

Figure A.3 The average area under the curve (AUC) scores for each level in (a) spatial modeling region, (b) environmental variable subset, and (c) statistical modeling method are provided. AUC values were calculated by using an independent presence and absence dataset from Moskwik (2014). For species codes see Table 3.1. Models were built on the following backgrounds: local convex hull (LCH), LCH buffered by 4 km (LCH4), minimum convex polygon (MCP), MCP buffered by 4 km (MCP4), and MCP4 excluding 2km around presence points (SQ). Environmental variable subsets 0-3 were created by an automated procedure and subsets 4-6 were selected from the literature. For the statistical modeling method the algorithms were generalized additive models (GAM), generalized boosted models (GBM), generalized linear models (GLM), multivariate adaptive regression splines (MARS), and random forest (RF).

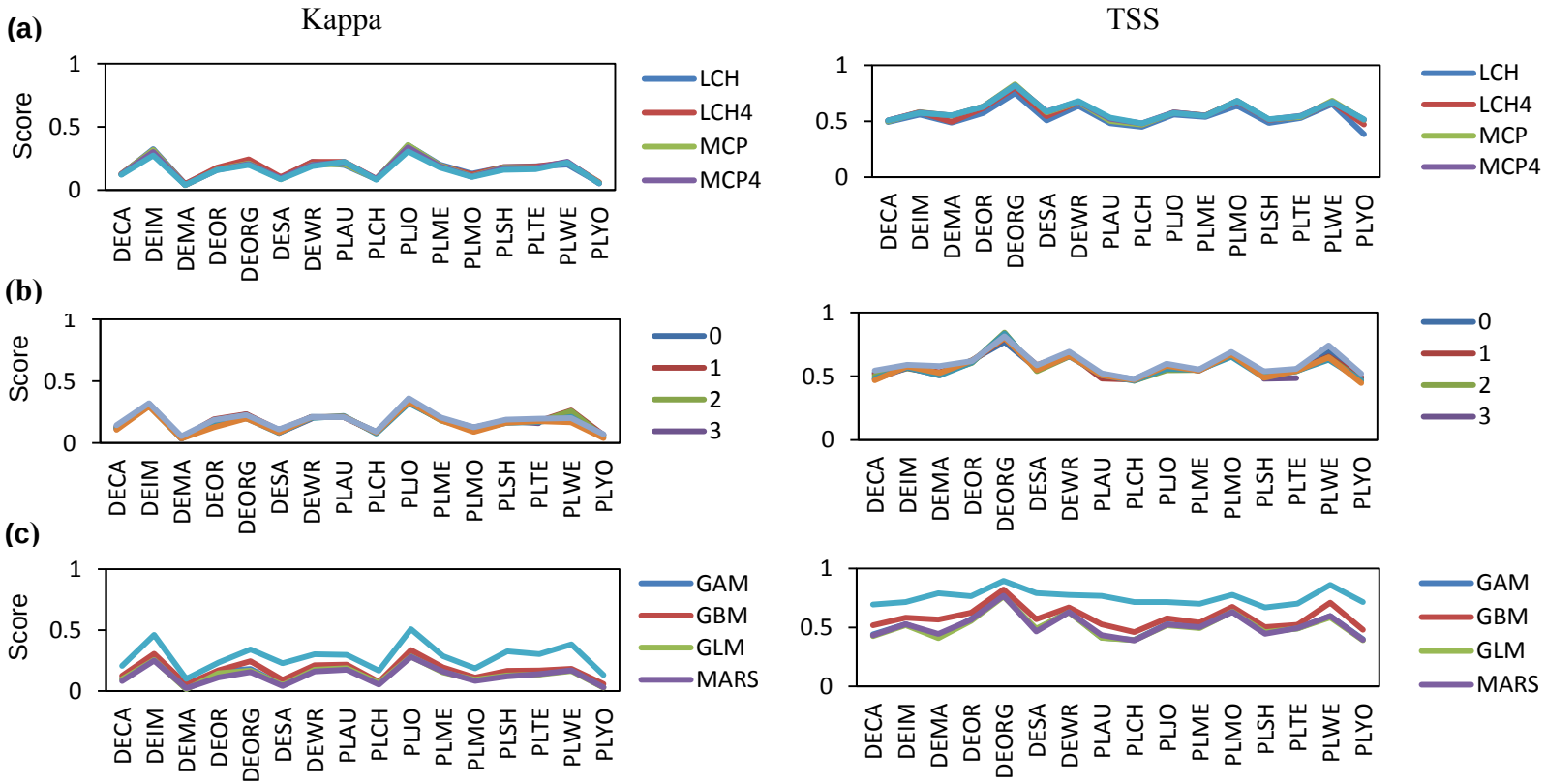

Figure A.4 The average kappa and true skill statistic (TSS) scores for each level in (a) spatial modeling region, (b) environmental variable subset, and (c) statistical modeling method are provided. Kappa and TSS values were calculated on the 4 km buffered minimum convex polygon (MCP4) background. For species codes see Table 3.1. Models were built on the following backgrounds: local convex hull (LCH), LCH buffered by 4 km (LCH4), minimum convex polygon (MCP), MCP4, and MCP4 excluding 2km around presence points (SQ). Environmental variable subsets 0-3 were created by an automated procedure and subsets 4-6 were selected from the literature. For the statistical modeling method the algorithms were generalized additive models (GAM), generalized boosted models (GBM), generalized linear models (GLM), multivariate adaptive regression splines (MARS), and random forest (RF).

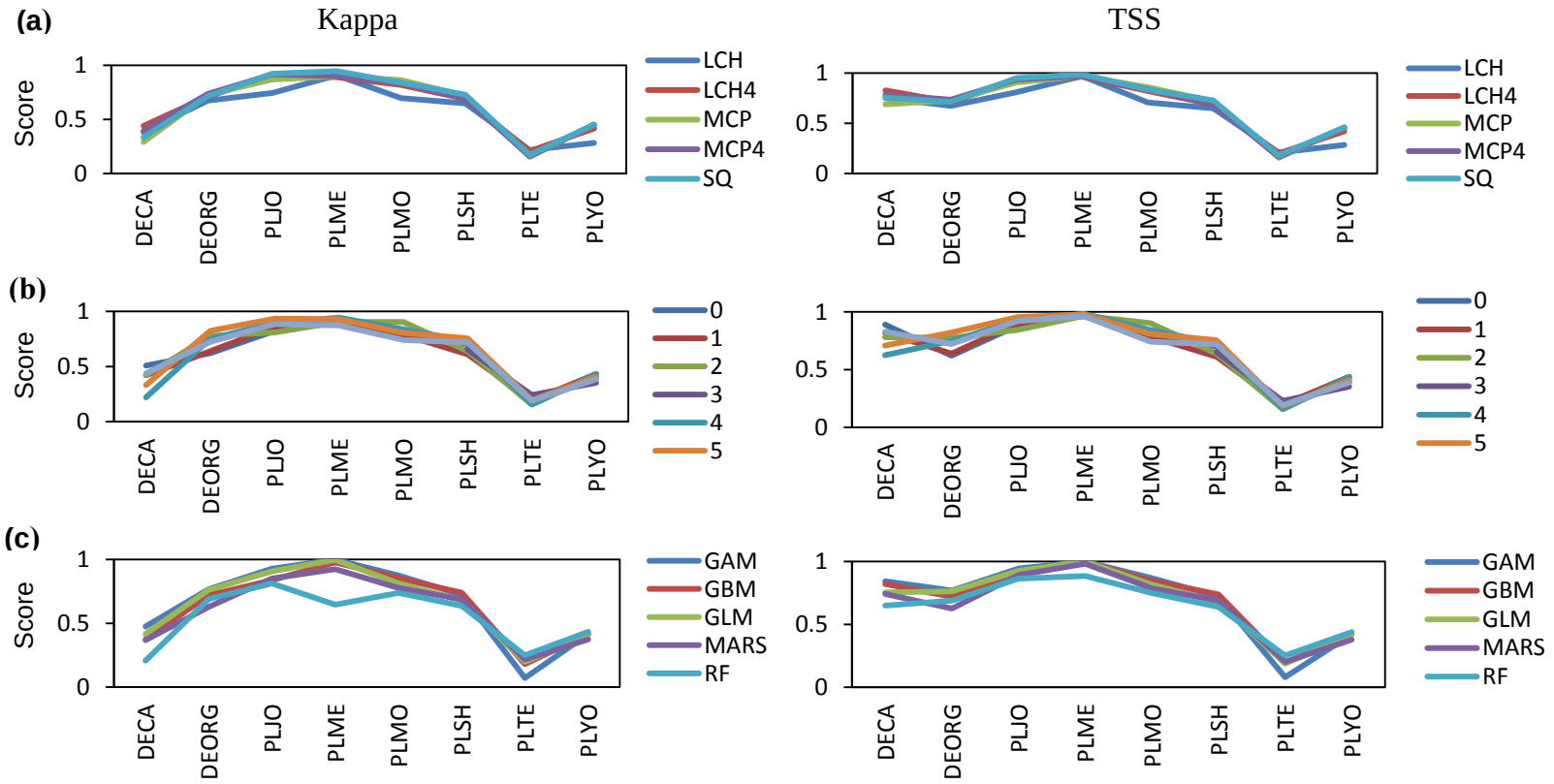

Figure A.5 The average kappa and true skill statistic (TSS) scores for each level in (a) spatial modeling region, (b) environmental variable subset, and (c) statistical modeling method are provided. Kappa and TSS values were calculated by using an independent presence and absence dataset from Moskwik (2014). For species codes see Table 3.1. Models were built on the following backgrounds: local convex hull (LCH), LCH buffered by 4 km (LCH4), minimum convex polygon (MCP), MCP buffered by 4 km (MCP4), and MCP4 excluding 2km around presence points (SQ). Environmental variable subsets 0-3 were created by an automated procedure and subsets 4-6 were selected from the literature. For the statistical modeling method the algorithms were generalized additive models (GAM), generalized boosted models (GBM), generalized linear models (GLM), multivariate adaptive regression splines (MARS), and random forest (RF).

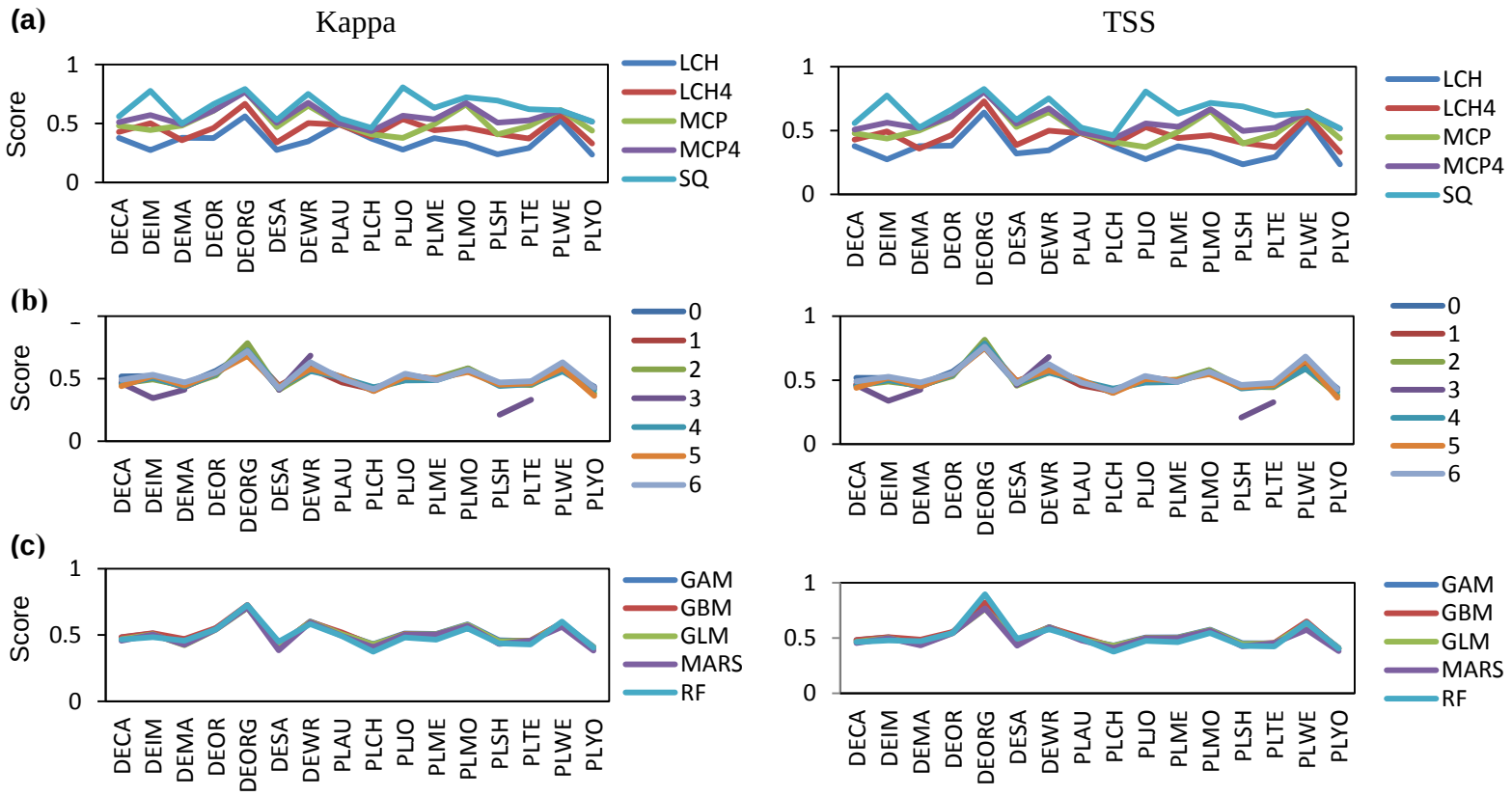

Figure A.6 The average kappa and true skill statistic (TSS) scores for each level in (a) spatial modeling region, (b) environmental variable subset, and (c) statistical modeling method are provided. Kappa and TSS values were calculated using the withheld 20% 'test' data. For species codes see Table 3.1. Models were built on the following backgrounds: local convex hull (LCH), LCH buffered by 4 km (LCH4), minimum convex polygon (MCP), MCP buffered by 4 km (MCP4), and MCP4 excluding 2km around presence points (SQ). Environmental variable subsets 0-3 were created by an automated procedure and subsets 4-6 were selected from the literature. For the statistical modeling method the algorithms were generalized additive models (GAM), generalized boosted models (GBM), generalized linear models (GLM), multivariate adaptive regression splines (MARS), and random forest (RF).

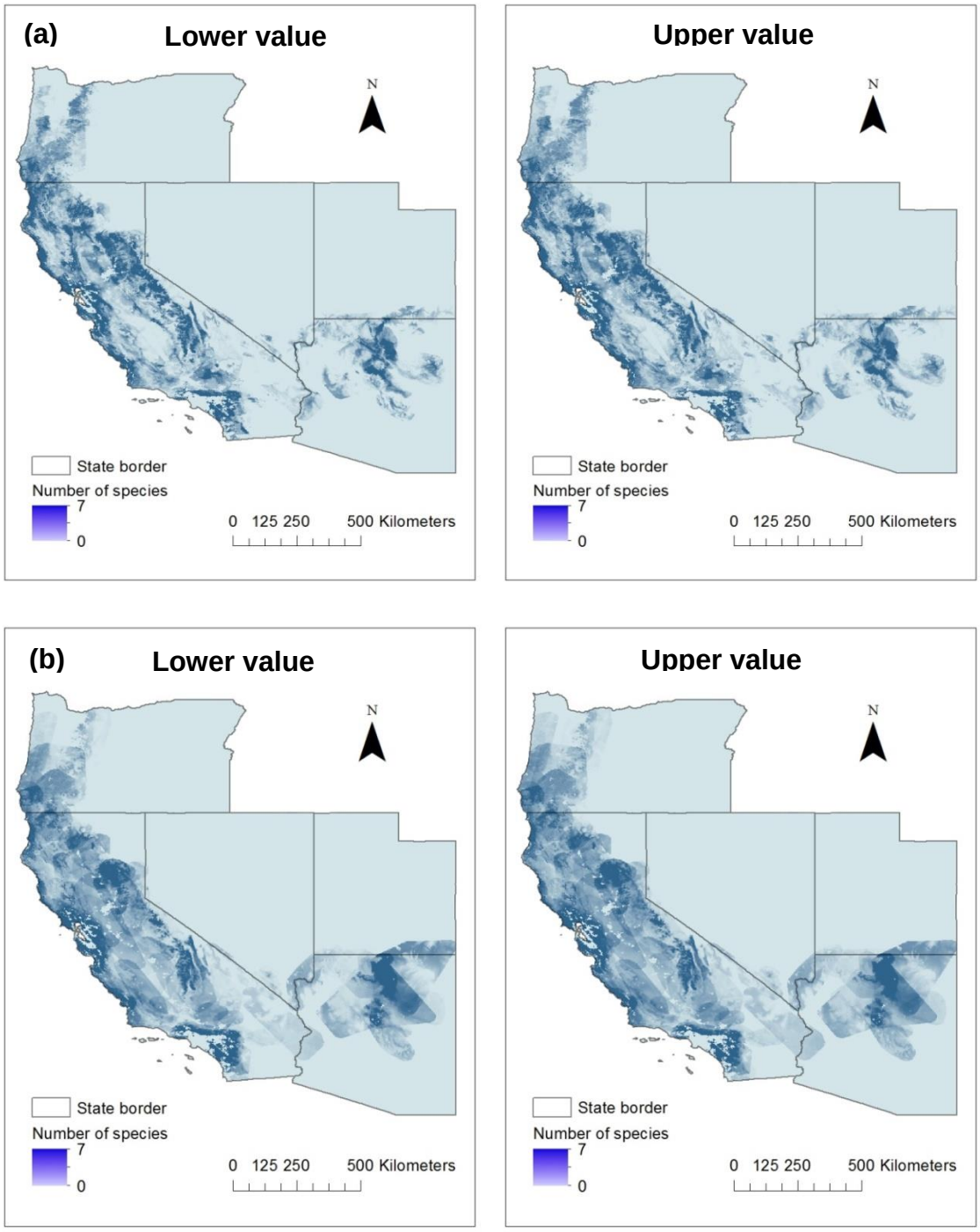

Figure A.7 90% confidence intervals for the 'realized' ranges of 164 species endemic to the southwest United States for the A) current and B) future time periods. Future projections assume limited migration of 25 km from current range boundaries.

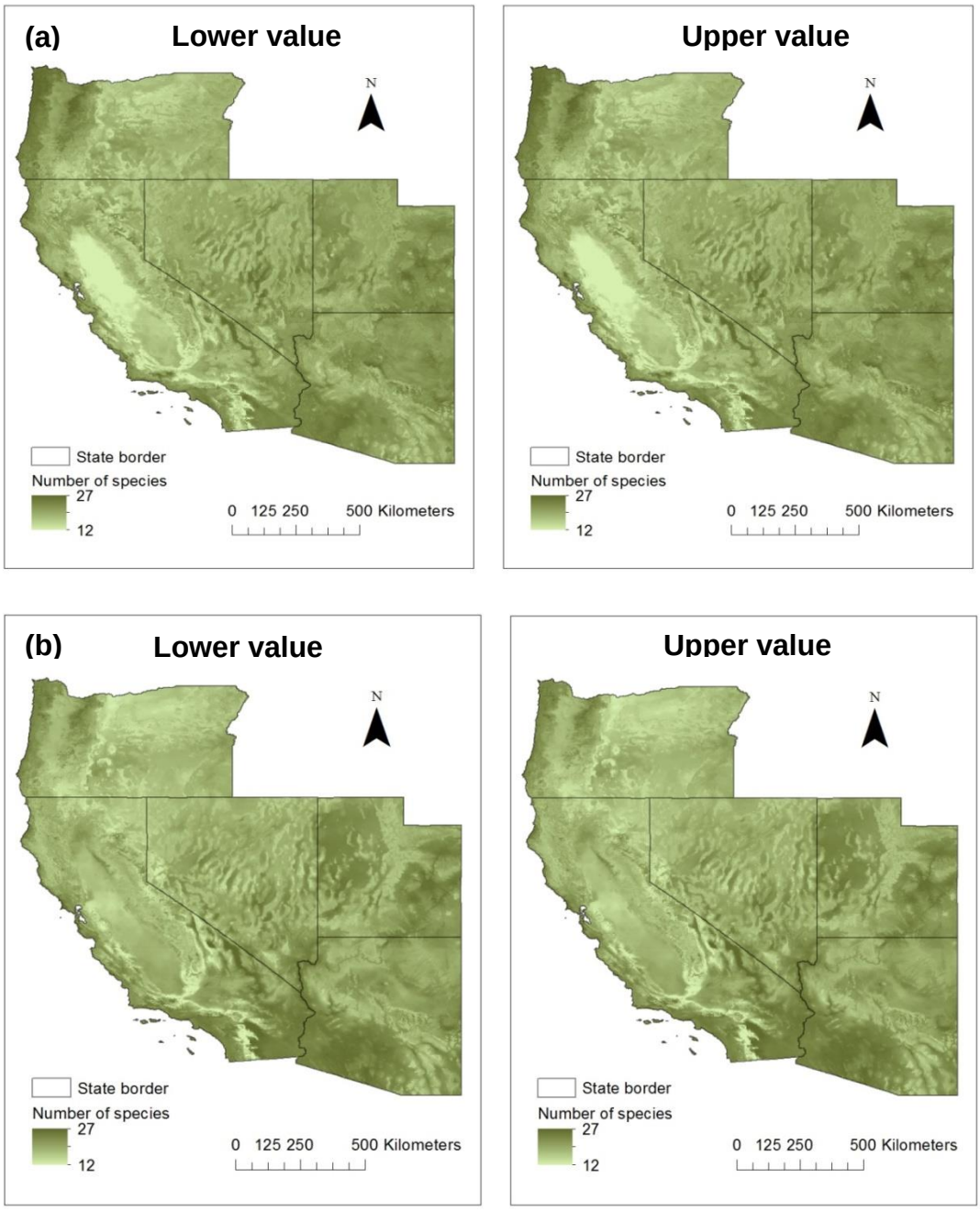

Figure A.8 90% confidence intervals for the 'potential' ranges of 164 species endemic to the southwest United States for the A) current and B) future time periods. The 'potential' range encompasses all climatically suitable regions in the southwestern United States, regardless of whether it is occupied by the species. Additionally, I assume unlimited future migration.

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Vita

Matthew Moskwik obtained Bachelor and Master of Science degrees in biology from Eastern Washington University in 2001 and 2004, respectively. Subsequently, he conducted field research abroad in Sierra Leone and Costa Rica on tropical bird communities. Upon returning to the United States, Matthew worked at The Nature Conservancy (TNC) and Wildlife Habitat Council (WHC). At TNC he coordinated the ivory-billed woodpecker search effort for South Carolina. For WHC he wrote wildlife conservation plans and educational programs for the business community in Houston, Texas. In 2009 Matthew enrolled in a graduate program in Ecology, Evolution, and Behavior at the University of Texas at Austin, with Camille Parmesan as his supervisor. Matthew's dissertation research focuses on past and future anthropogenic impacts to plethodontid salamanders in the southern Appalachian Mountains. Additionally, he is involved in an effort with the National Center for Atmospheric Research and Rand Corporation to account for and quantify the uncertainty in future projections from species distribution models.

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